GENECOLOGICAL STUDIES ON THE VARIATION OF IMPERATA CYLINDRICA,A PERENNIAL WEED(Dissertation_全文)

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Contents

Chapter 1. Introduction

Imperata cylindrica (Linn.) Beauv., distributed widely in the tropics and the warm temperate zone of the world, is regarded as one of the ten world's worst weeds (Holm et al., 1977). Hubbard (1944) reviewed the taxonomy and distribution of this species. Five taxonomic varieties were distinguished by certain morphological features, such as the size of culms, leaves, and inflorescences. I. cylindrica var. major (Nees) C. E. Hubbard is widespread in the tropical and warm temperate regions of Asia, Oceania, and the eastern part of tropical Africa. In the Southeast Asia, this taxon, called "Alang-alang" or "Lalang", is the most noxious weed in oil palm, rubber, coconut, tea, citrus, and the other kinds of plantations. This weed also infests the very large areas where shifting cultivation is practiced (Holm et al., 1977). It was introduced into the southern United States of America as packing material in a shipment from Japan and a potential pasture grass from the Philippines early in this century, and has become a serious weed in pastures, nurseries, pecan plantations, and lawns (Patterson et al., 1980). I. cylindrica var. africana (Anderss.) C. E. Hubbard is distributed over the north of

tropical regions and southwards of Africa. This variety is a serious weed in tea, coffee, sisal, and the other kinds of fields (Terry, 1984). Var. europaea (Anderss.) Aschers. et Graebn. occurs mainly in the Mediterranean region, the Nearer East, and Central Asia. Var. condensata (Steud.) Hack. ex Stuckert grows in the coastal region of Chile and Argentina. Var. latifolia (Hook. fil.) C. E. Hubbard is distributed in the northern part of India.

In Japan, I. cylindrica, called "Chigaya", is distributed widely from Hokkaido to Okinawa Prefecture. Honda (1930) divided I. cylindrica of Japan into two varieties, based on the hairs at the node of culm: Var. koenigii with hairs and var. genuina without ones. Furthermore, var. genuina is subdivided into two formae mainly based on the colour of stigma: Form. typica has deep reddish brown or dark purple stigma; form. pallida has whitish brown one.

In citrus, tea, and the other kinds of the fields in the southwestern parts of Japan, this species is noxious and its control is very difficult. This rhizomatous weedy grass grows vigorously and its shoots sprout all over the year except the coldest season from November to February. It flowers in mid-May and matures seeds in late June of the rainy season. The seed germinates quickly under the moist condition at 25 to 30 ℃, for the seed has no dormancy (Matumura et al., 1983). The rhizome has a bud on each

node and it is a main vegetative reproductive organ of this species. When the rhizome is cut off from the mother plant, those buds grow up to the shoots immediately. The tips of rhizome also become shoots. These sexual and vigorous asexual reproductions are surely one of the factors of the difficulty in controlling them and of troublesome.

For establishing rational weed control program, it seems to be necessary to clarify intraspecific variation, as reviewed by Kobayashi (1984). In Japan, only a few such studies have been reported. Sakamoto (1961, 1978) reported the early ecotype of Agropyron tsukushiense (Honda) Ohwi var. transiens (Hack.) Ohwi, adapted to the idle lying paddy fields. In Alopecurus aequalis Sobol. var. amurensis (Komar.) Ohwi (Matumura, 1967), the genetic differences between up-land and low-land type were found. Kobayashi and Ueki (1979, 1983) recognized four intraspecific groups of Eleocharis kuroguwai Ohwi, which are the irrigation pond, the plain, the paddy field, and the Oshima Island group, based on the plant type and tuber formation time. In above three species, the relationships of the genetic differentiation and the adaptive characteristics to each habitat were well explained.

Through the collection of I. cylindrica in Japan for genecological study, the wide variation within species was

suggested. A male sterile biotype in foredune of the southern part of the Kii Peninsula was reported (Tominaga et al., 1985) and also the latitudinal cline was found in the phenology and plant size of this species in Japan (Tominaga et al., 1986). Matumura et al. (1980, 1983, 1984) reported the early flowering type indigenous to the Nohbi Plain in Central Japan. This type was distinguished from the common one by its glabrous node, early flowering habit, and heavier caryopsis weight. The morphological variation of this species was reported in Malaysia (Santiago, 1976) and in Iraq (Al-juboory and Hassawy, 1980). These reports indicate that I. cylindrica in Japan has wide intraspecific variation.

In this thesis, the genecological studies on the variation of I. cylindrica were conducted from the following four different standpoints: 1) **Dry matter production** The seasonal change in the standing crop of I. cylindrica var. koenigii grassland in the Kii-Ohshima Island, located at the southern extremity of the Kii Peninsula, was clarified. 2) **Intra- and inter-populational variation in the Kii-Ohshima Island** To study intraspecific variation, it is necessary to clarify the variation within population firstly. The intra- and inter-populational variation in the plant size, morphology, pollen fertility, and seed set percentage was surveyed in 11 populations in the Kii-

Ohshima Island. 3) **Differences between inland and foredune populations in the Kii Peninsula** For the discussion of the relationships between the genetic differences among populations and the mode of adaptation to each habitat, the plant size, morphology, pollen fertility, and seed set percentage were measured on 17 inland populations and 16 foredune populations of I. cylindrica var. koenigii in the Kii Peninsula. 4) **Geographical variation in Japan** To clarify the distribution and geographical variation of this species in Japan, the phenology, plant size, and morphology of clones collected from Hokkaido to Okinawa Prefecture were investigated.

Chapter 2. Seasonal change of the standing crop of *Imperata cylindrica* var. *koenigii* grassland in the Kii-Ohshima Island of Japan

INTRODUCTION

It is important to make clear the seasonal change in the dry matter production of weeds for establishing rational weed control program, but only a few studies on *Imperata cylindrica* (Linn.) Beauv. var. *koenigii* (Retz.) Durand et Schinz (Chigaya in Japanese) have been reported.

In the southwestern parts of Japan, this species grows vigorously and sprouts new shoots all over the year except winter. It heads in mid-May and one panicle can set more than five hundred seeds. The seed of this species has no dormancy (Matumura et al., 1983). The vegetative reproduction is made by rhizome. The tip of rhizome becomes shoot and when the rhizome is cut off from the mother plant, the bud on node of rhizome quickly becomes the shoot.

In this chapter, the seasonal change of the standing crop of *I. cylindrica* var. *koenigii* grassland in the abandoned field of the Kii-Ohshima Island was clarified.

MATERIALS and METHODS

Description of the investigated field

The seasonal change in the standing crop of I. cylindrica var. koenigii grassland was investigated in the about 30 x 20 m^2 abandoned field (33°28'N, 135°50'E, 50 m above the sea level) of the Kii-Ohshima Island located at the southern extremity of the Kii Peninsula. This field was abandoned after sweet potato (Ipomoea batatas Lam.) had been cultivated in 1940's. I. cylindrica var. koenigii grows densely and covers almost all area of this field (Fig. 1). For using this grass weed as mulching material, uncyclic mowing is conducted several times a year. The last mowing before the beginning of the investigation was practiced in late April, 1980.

Measurements of the standing crop

The measurements of the standing crop in three 50 x 50 cm^2 quadrats were conducted at the intervals of about one month from June 14th, 1980 to May 18th, 1981. Plant height, number, and coverage of each species were investigated. The coverage was assessed according to Penfound and Howard (1940). Aerial parts were cut into every 10 cm stratum from the ground surface by the stratified clipping

Fig. 1. View of the investigated field on May 14, 1981.

method of Monsi and Saeki (1953). After sampling, the aerial parts of each stratum were divided into leaf blades, leaf sheaths, petioles, culms, stems, panicles, and flowers; they were dried up at 80°C for 48 hours, and then dry matter weight of each organ in each stratum was measured individually. The rhizomes of I. cylindrica var. koenigii were sampled in every 5 cm layer from the ground surface. Rhizome dry matter weight of each layer was investigated at each measurement.

The horizontal distribution of rhizome was also clarified in the 2 x 2 m^2 quadrat and the branching pattern of a rhizome was studied.

RESULTS and DISCUSSION

Thirty-two species were found in the three quadrats of the abandoned field during observation (Table 1). Fig. 2 shows the horizontal distribution of the species in the 50 x 50 cm^2 quadrat at the beginning of the investigation, on June 14th, 1980. Imperata cylindrica var. koenigii grew densely and was dominant all over the year. Miscanthus sinensis Anderss. occupied less than 10% of the quadrat, Rumex acetosa Linn., Cassia nomame (Sieb.) Honda, Geranium thumbergii Sieb. et Zucc., and Paederia scandens (Lour.)

Table 1. Species and their coverage in the investigated field.

Species	Coverage* 1980. Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	1981. Jan.	Feb.	Mar.	Apr.	May
Imperata cylindrica var. koenigii	━	━	━	━	━	━	━	━	━	━	━	━
Miscanthus sinensis	━	━	━	━	━	━	━	━	━	━	━	━
Rumex acetosa	┅	━	━	━	━	━	━	━	━	━	━	━
Cassia nomame	━	━	━	━	━	━	━	━			─	─
Geranium thunbergii		┅	━	━	━	━	━	━			─	─
Paederia scandens var. mairei		┅	━	━	━	━	━	━	┅	━	━	━
Lactuca indica var. laciniata			━	━	━	━	━					
Pteridium aquilinum var. latiusculum										┄	┄	┄
Lophatherum gracile	┄	┄	┄	┄	┄	┄	┄	┄			┄	┄
Arundinella hirta	┄	┄	┄	┄	┄	┄	┄		┄	┄	┄	┄
Arthraxon hispidus			┄	┄	┄	┄	┄	┄		┄	┄	┄
Cyperus cyperoides		┄	┄	┄	┄	┄	┄	┄				
C. rotundus	┄	┄	┄	┄	┄							
Carex sp.											┄	┄
Scilla scilloides		┄	┄	┄	┄	┄						
Ophiopogon japonicus	┄	┄	┄	┄	┄	┄	┄	┄	┄	┄	┄	┄
Dioscorea japonica	┄	┄	┄	┄	┄	┄	┄					
Stephania japonica		┄	┄	┄	┄	┄	┄					
Corydalis heterocarpa var. japonica										┄	┄	┄
Potentilla freyniana	┄	┄	┄									
Kummerovia striata	┄	┄	┄	┄	┄	┄	┄					
Vicia sepium	┄	┄	┄	┄	┄	┄	┄		┄	┄	┄	┄
Oxalis corniculata	┄	┄	┄									
Viola mandshurica										┄	┄	┄
Hydrocotyle sibthorpioides	┄	┄	┄	┄	┄	┄	┄	┄	┄	┄	┄	┄
Lysimachia clethroides	┄	┄	┄									
Justicia procumbens var. leucantha	┄	┄	┄	┄	┄	┄	┄					
Lonicera japonica	┄	┄	┄	┄	┄	┄	┄			┄	┄	┄
Patrinia scabiosaefolia			┄	┄	┄	┄						
Solidago virga-aurea var. asiatica			┄	┄	┄	┄						
Artemisia princeps	┄	┄	┄	┄	┄	┄	┄	┄	┄	┄	┄	┄
Ixeris dentata	┄	┄	┄	┄	┄							

* ━: Coverage, 76 to 100%; ─: 6 to 25%; ─: 1 to 5%; ┄: less than 1%.

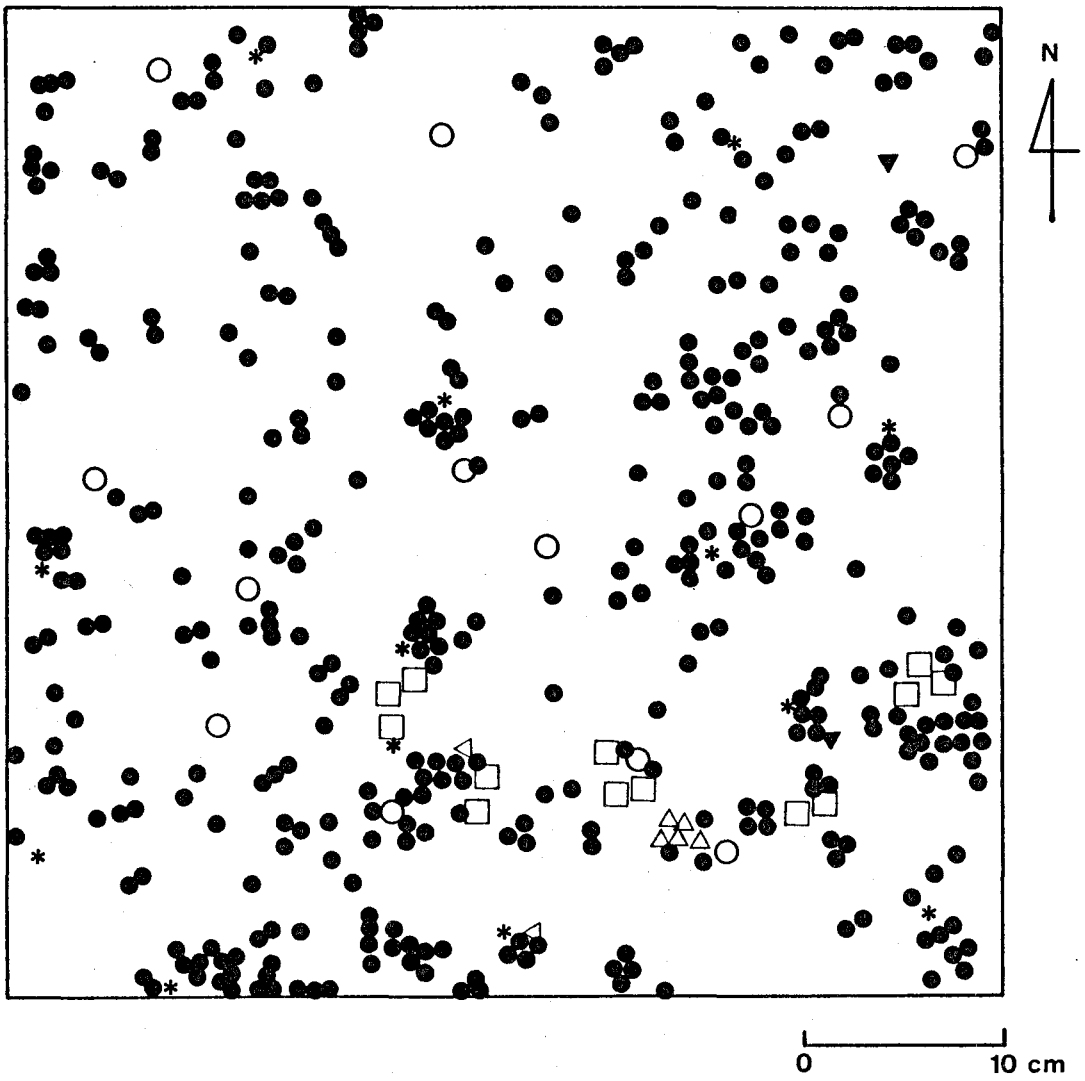

Fig. 2. Horizontal distribution of the species in the 50 x 50 cm^2 quadrat on June 14, 1980.

●: Imperata cylindrica var. koenigii; □: Miscanthus sinensis; ◁: Rumex acetosa; ▼: Cassia nomame; △: Ophiopogon japonicus; ○: Lonicera japonica; ∗: the other species.

Merrill var. mairei (Léveillé) Hara possessed less than 5%, and the coverage of the other 26 species was small. No seedlings of I. cylindrica var. koenigii were observed.

As shown in Fig. 3, I. cylindrica var. koenigii grew very swiftly. The plant height had reached 89.7 cm and a part of lower leaves had died in June 14th, 1980. The canopy of the quadrat consisted of five species, I. cylindrica var. koenigii, Miscanthus sinensis, and three volubile species, Paederia scandens var. mairei, Lonicera japonica Thunb., and Stephania japonica (Thunb.) Miers. The standing crop of the other 27 species was very small, less than 5% of the total standing crop. On February 16th, 1981, the aerial parts of I. cylindrica var. koenigii almost died.

The standing crop in this field reached the peak in January, 883 g/m^2 and 772 g/m^2 of it was occupied by I. cylindrica var. koenigii. 883 g/m^2 was higher than those (376 to 793 g/m^2) of the fields where Miscanthus sinensis dominated (Numata et al., 1966; Koike, 1969; Koike and Yoshida, 1969).

The standing crop of rhizome increased notably in September to November accompanied with the large amount of the standing crop of living leaf blade in September and October. The dry matter weight of dead leaf blade and leaf sheath showed the maximum value in January and that of

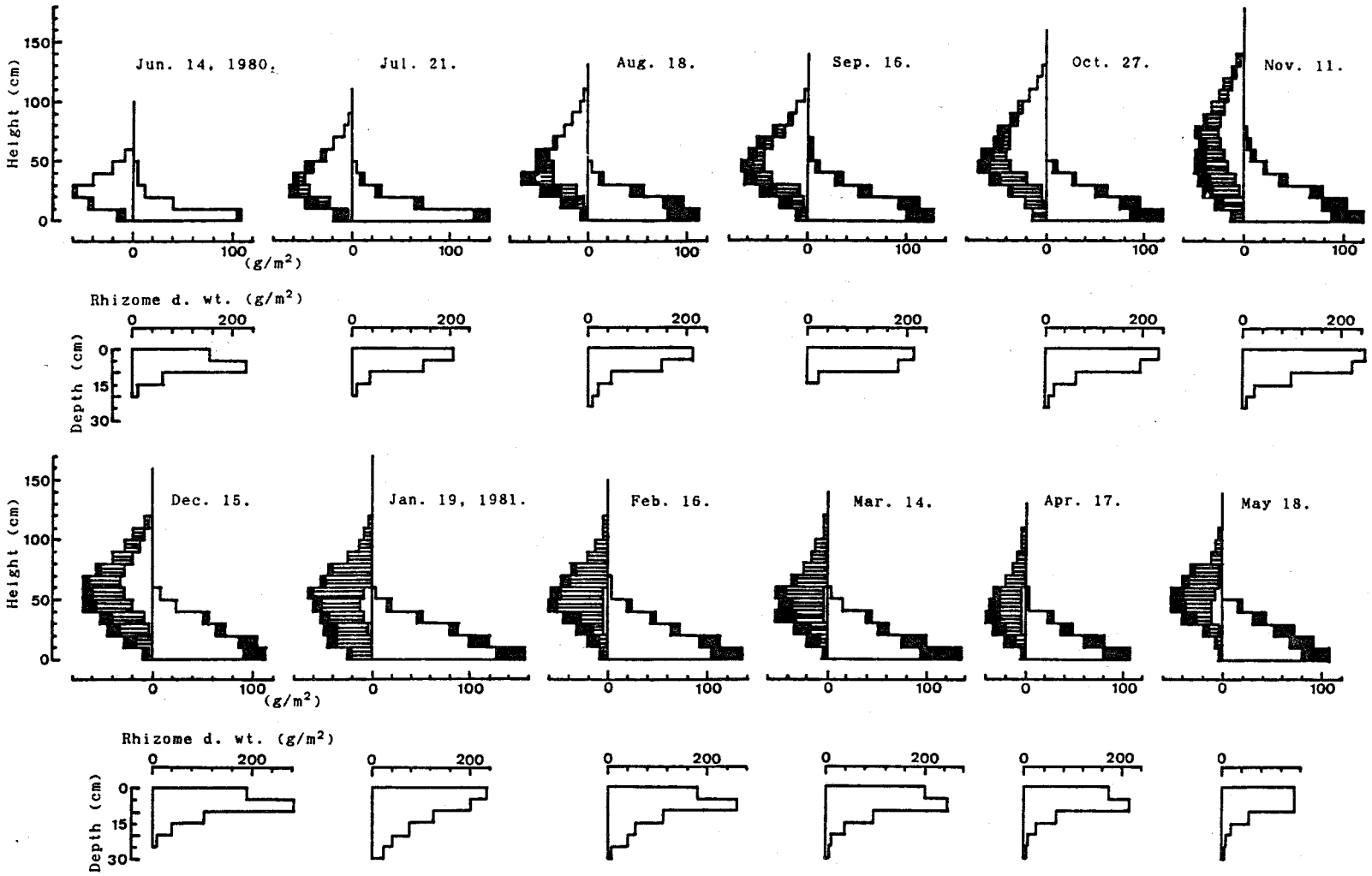

Fig. 3. Seasonal change of productive structure of the Imperata cylindrica var. koenigii community.

Dry weights of photosynthetic part are shown in the left side of longitudinal line and non-photosynthetic part in the right side. ▭: I. cylindrica var. koenigii; ▤: dead leaf blade of I. cylindrica var. koenigii; ■: the other species.

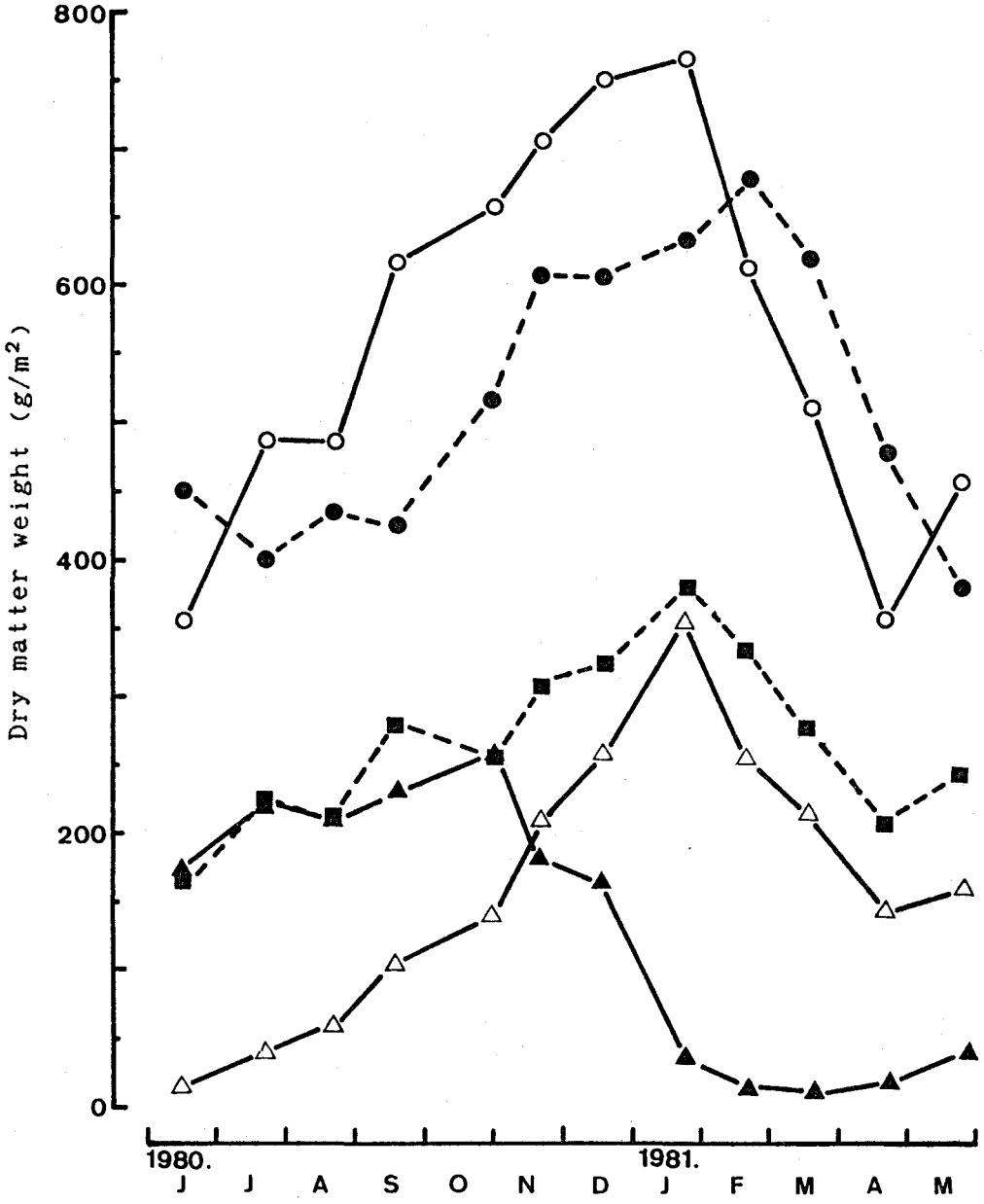

Fig. 4. Seasonal changes in the standing crop of each organ of Imperata cylindrica var. koenigii.

▲: living leaf blade; △: dead leaf blade;
●: rhizome; ■: leaf sheath, culm, and panicle;
○: total aerial parts.

rhizome reached in February, 653 g/m^2 (Fig. 4), being one month later in the aerial part. This may be attributed to that the energy of aerial parts was translocated into rhizomes. The standing crop of rhizome decreased on and after March, when the new shoots sprouted.

Soil texture of the quadrat was as follows: The 0 to 14 cm layer from the surface of the ground was composed of black loam, 14 to 17 cm layer of black loam containing red clay, 17 to 21 cm layer was red clay, and 21 to 40 cm layer of red clay containing conglomerates (Fig. 5). The greater parts of rhizomes of I. cylindrica var. koenigii were distributed in the 0 to 30 cm deep in soil; they were dense in the 5 to 10 cm layer (Figs. 3 and 5). The rhizomes of this weed got tangled together complexly and densely in the field (Fig. 6). The branching pattern of a rhizome was surveyed. As a part of rhizome was decomposed or broken, the branching pattern could not be detected completely; but the rhizome which spread at least more than 1.5 x 1.9 m branched complicatedly (Fig. 7). The inter-node length of rhizome was 2.0 to 2.5 cm but the one of the proximal part was very short, 0.1 to 0.3 cm. It may be useful for the control of this weed to classify the rhizomes to age or size classes, but it was not possible to do so because to distinguish a rhizome from another was impossible. In the future, however, it will be necessary to clarify the con-

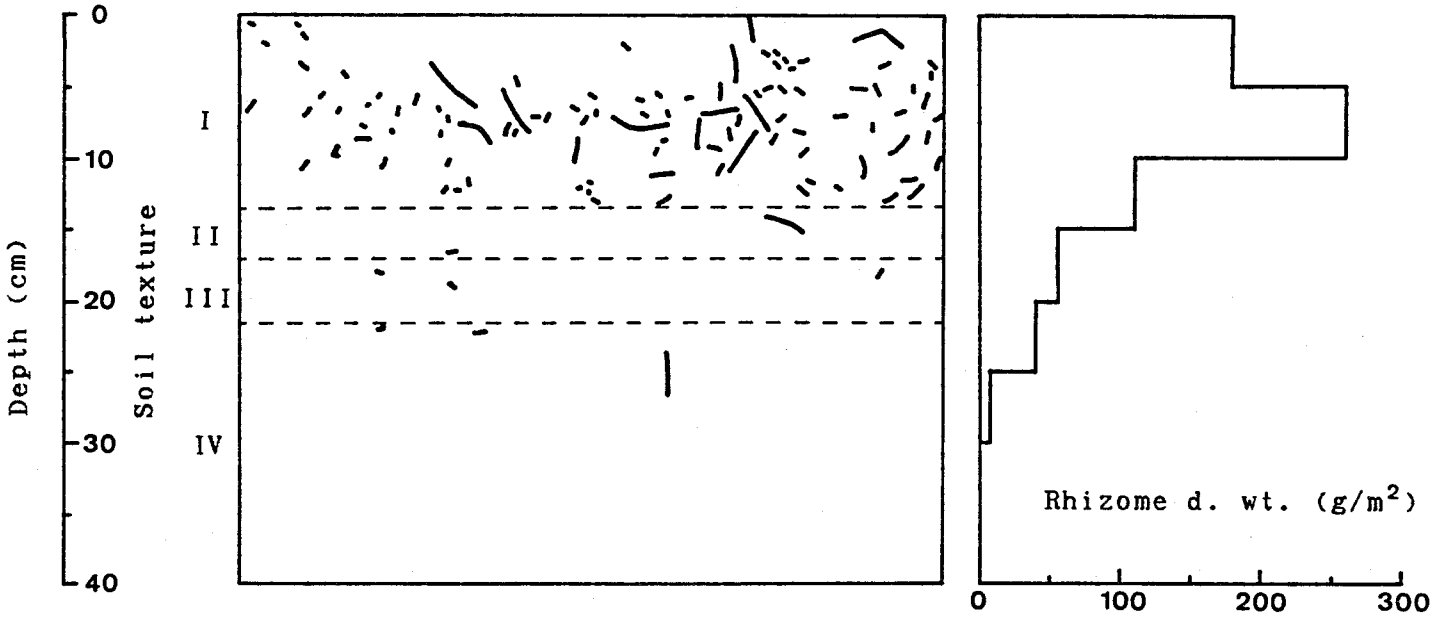

Fig. 5. Vertical distribution of rhizome of Imperata cylindrica var. koenigii on March 1, 1981.

Soil texture I: black loam; II: black loam containing red clay; III: red clay; IV: red clay containing conglomerates.

Fig. 6. Horizontal distribution of rhizomes of Imperata cylindrica var. koenigii on March 1, 1981.

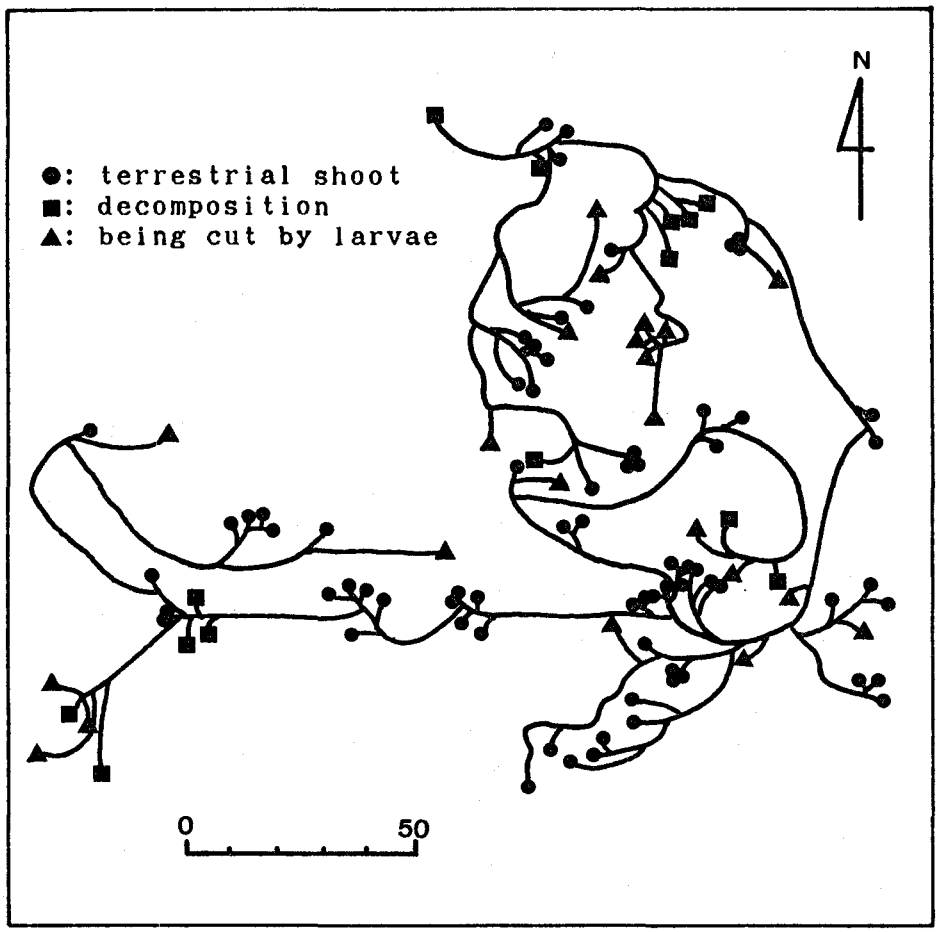

Fig. 7. Branching pattern of a rhizome of Imperata cylindrica var. koenigii.

The digging and the observation were practiced on March 1, 1981.

stitution of age or size class of rhizome in the natural population.

The large biomass of rhizome may enhance the rapid regrowth and vigorous vegetative reproduction of this weed. The dominance of I. cylindrica var. koenigii in this field is due to the several mowing in a year. The reasons for the difficulty in controlling this weed species are considered to be the complicated branching in various directions and vertically and horizontally wide distribution of rhizome.

Chapter 3. Intra- and inter-populational variation of Imperata cylindrica var. koenigii in the Kii-Ohshima Island of Japan

INTRODUCTION

A few genecological studies on weeds of arable lands were reported, as mentioned by Kobayashi (1984). In spite of the difficulty in the control of Imperata cylindrica (Linn.) Beauv. var. koenigii (Retz.) Durand et Schinz, there have been only a few studies on its intraspecific variation. Matumura et al. (1980, 1983, 1984) reported the early flowering type of this weed in the Nohbi Plain, Central Japan. This type was distinguished from the common type by its glabrous node, large caryopsis, and early flowering habit. In the way of collection of this weed species in Japan for the genecological studies, interclonal variation was found (Tominaga et al., 1985, 1986). To study the variation of this species, it is necessary to clarify the mode of intra- and inter-populational variation firstly.

In this study, the intra- and inter-populational variations of I. cylindrica var. koenigii in 11 populations of

the Kii-Ohshima Island (33° 28'N, 135° 50'E, 9.91 km^2), located at the southern extremity of the Kii Peninsula, were investigated.

MATERIALS and METHODS

Collection of clones

From the 11 populations of the Kii-Ohshima Island, which were 5 roadside populations, 2 abandoned fields, 1 orchard garden, 2 lawns, and 1 foredune (Fig. 8), each five clones being as apart as possible from one another were collected by 1982. In total, 55 clones from 11 populations were planted individually in the clay pots (20 cm diameter x 19 cm depth, about 6000 cm^3) filled with clay loam. Fertilizers, N 10, P 10, and K 10 Kg/10a were applied basically. They were raised at the Subtropical Plant Institute of Kyoto University in the Kii-Ohshima Island.

Morphological characters and pollen fertility

The rhizomes of each clone planted in the clay pot by 1982 were dug up and then cut into about 10 cm long pieces with 10 to 12 nodes on April 18th, 1983. Cut rhizomes of each clone were kept on the vermiculite beds in a greenhouse. Five ramets of about 10 cm long with three leaves

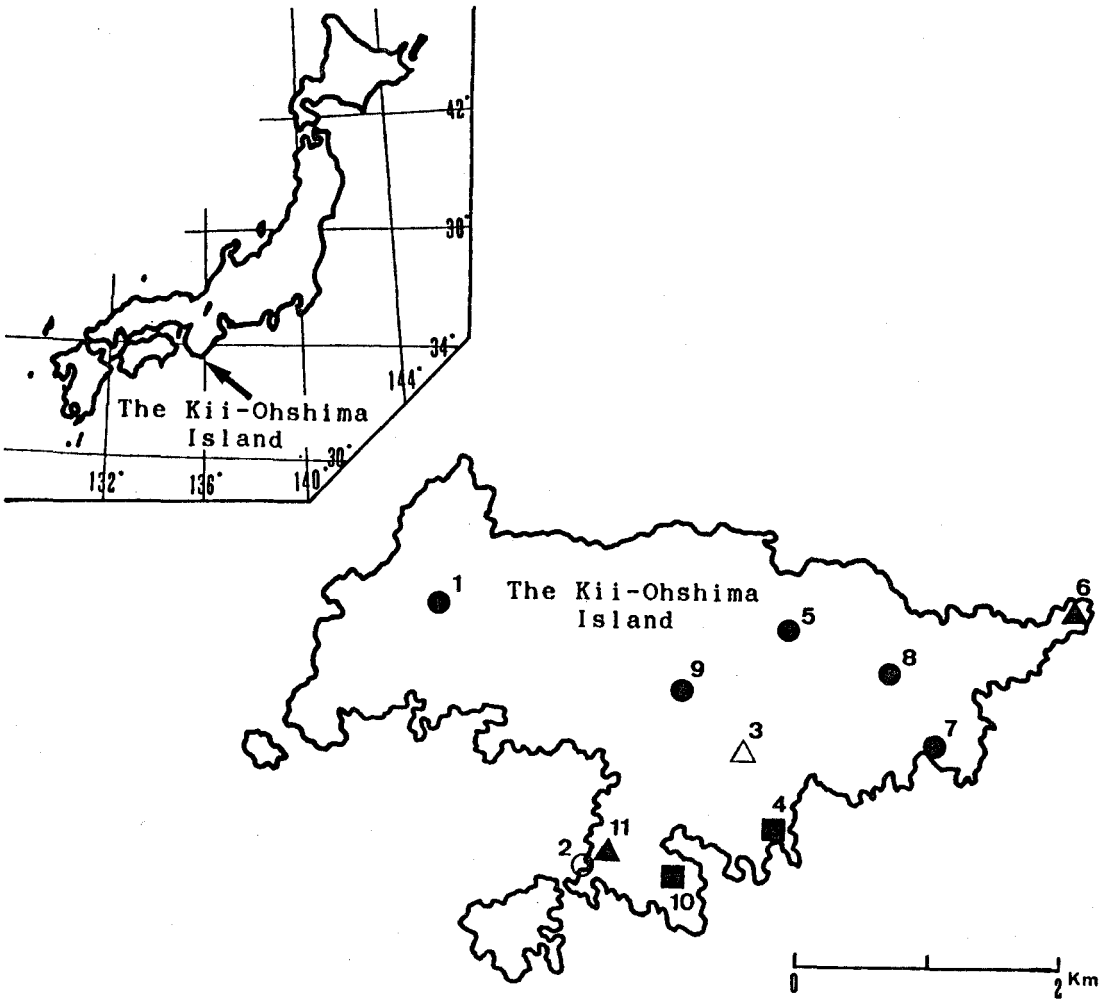

Fig. 8. Investigated 11 populations of Imperata cylindrica var. koenigii in the Kii-Ohshima Island.

●: roadside; ○: foredune; △: orchard garden;
▲: lawn; ■: abandoned field.

from each clone were planted in the clay pots (20 cm diameter x 19 cm depth) filled with clay loam on June 10th, individually. In total, 275 ramets (5 ramets x 5 clones x 11 populations) were used for this experiment. Fertilizers, N 10, P 10, K 10 Kg/10a were applied basically. In mid-November, all ramets were dug up. Plant length, number of shoots and rhizomes, diameter and length of rhizomes were measured. Each ramet was separated into leaf blades, leaf sheaths, roots, and rhizomes to be dried up at 80 °C for 48 hours and then their dry matter was weighed.

The pollen fertility of each clone in the clay pot was investigated by aceto-carmine staining in mid-May, 1983. To compare the pollen fertilities observed in cultivated ramets with those observed in the original habitats, the pollen fertility in each original habitat was also surveyed as for ten panicles.

Seed set percentage and 100 kernel weight

The seed set percentages of cultivated clones under open and bagged condition were investigated. Each half number of heading panicles in the pot were bagged on May 2nd, 1983 and the residuals were kept opened. On mid-June, seed set percentage and one hundred kernel weight were measured.

This species is protandrous and wind pollinated plant.

Therefore, also in the natural population, the seed set percentage under open and bagged condition was investigated. Ten panicles of each natural population were randomly sampled in mid-June from 1982 to 1984. The number of setting seeds, all florets, and one hundred kernel weight were measured for each panicle. Fifty panicles were bagged on May 4th, 1983 and after 42 days the panicles were collected and seed set percentage was surveyed.

RESULTS

Morphological characters and pollen fertility

Statistically significant differences among populations were shown in the plant length, total dry matter weight, number of shoots, total rhizome length, rhizome dry matter weight per total rhizome length, anther size, and the dry matter partitioning ratio to rhizome (the arcsin $\sqrt{\text{percentage}}$ transformation was made for statistical calculation), but not within population (Table 2).

The glume length was negatively related to the distance from seashore, as shown in Fig. 9, but in the other characters such tendency was not found.

The clones from the foredune population (No. 2) showed especially different morphology, compared with the other

Table 2. Analysis of variance for seven characters under cultivated condition in 1983.

Source of variation	D.f.	Meansquares						
		Plant length	Total dry weight	Number of shoots	Total rhizome length	Weight/length of rhizome	Anther width	Dry matter partitioning ratio to rhizome
Among populations	10	101.61 **	64.47 **	19.57 **	49287.3 **	0.1986 **	0.2393 **	18.26 **
Within population	4	74.48	34.24	5.65	20896.5	0.2214	0.0009	8.43
Error	40	39.47	23.49	8.43	16526.2	0.0854	0.0020	5.26

a: arcsin $\sqrt{\text{percentage}}$ transformation was made for statistical calculation.
**: significant at 1% level.

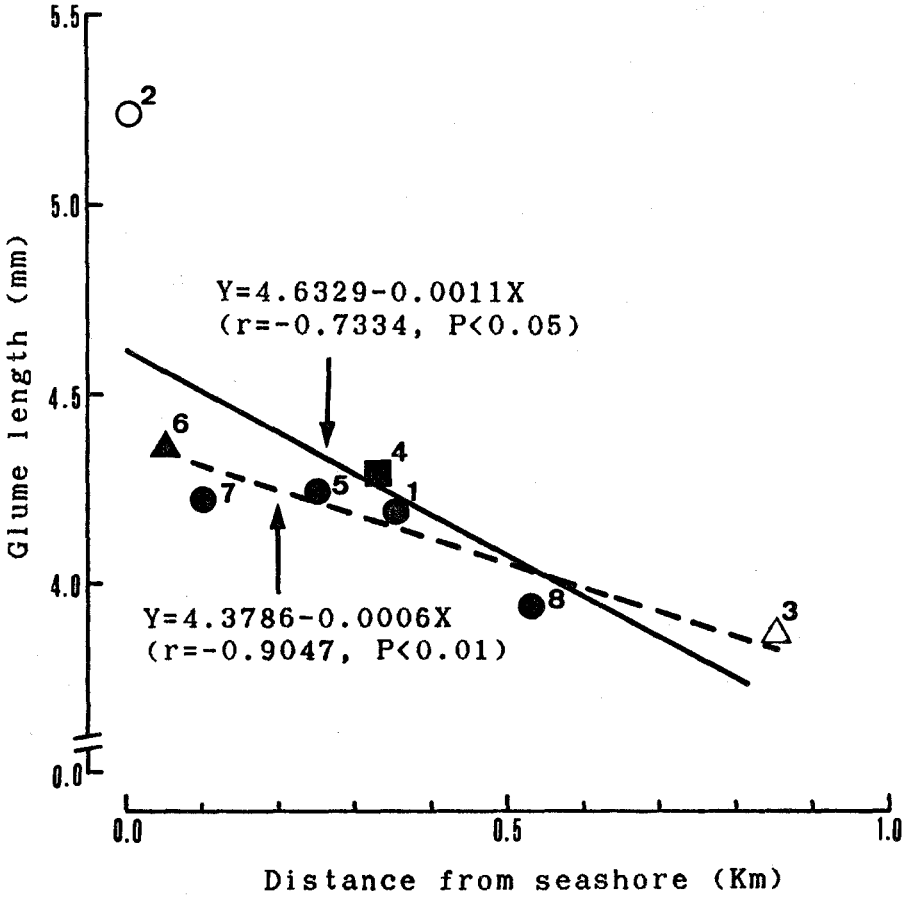

Fig. 9. Relations between glume length of Imperata cylindrica var. koenigii and distance from seashore.

Symbols and numbers are the same as in Fig. 8.
———: the data of all populations.
-----: the data except No. 2.

ten populations. They had larger number of shoots and rhizomes, greater total rhizome length, longer glume, and smaller anther than the others (Tables 3 and 4; Fig. 9). The coefficient of variation (C.V.) of plant length, total dry matter weight, total rhizome length, number of shoots and rhizomes in population No. 2 were generally smaller than those of the other ten populations.

The pollen fertility of natural population indicated 94.08 to 99.15%, except population No. 2 (Table 5). Population No. 2 had a few fertile and sterile pollen grains in anther sacs but normal pistils as those of the other ten populations.

In cultivated condition, the pollen fertility was 94.80 to 99.50% except population No. 2 (Table 3). Those data corresponded with the one obtained in natural population studies. The size of anther of population No. 2 was extremely small (Table 3).

Seed set percentage and 100 kernel weight

The seed set percentages were investigated in seven populations (Nos. 1-4 and 6-8) in 1982, in nine populations (Nos. 1-7, 9, and 10) in 1983, and in 11 populations (Nos. 1-11) in 1984. The panicles of four populations (Nos. 5 and 9-11) in 1982 and two populations (Nos. 8 and 11) in 1983 were not produced, and the seed set percentage was not

Table 3. Variation of seed set percentage in open and self pollination, pollen fertility and 100 kernel weight under cultivated condition in 1983.

Population No.	Seed set percentage (%)		Pollen fertility (%)	100 kernel weight (g)	Anther	
	open pol.	self pol.			length (mm)	width (mm)
1	20.99[d]	0.00[d]	99.33±0.42	#	3.40±0.07	0.83±0.07
2	17.72±20.31*	0.10±0.18	/[a]	#	1.94±0.07	0.16±0.02
3	2.25[d]	0.17±0.19	98.42±0.73	#	2.44±0.10	0.82±0.05
4	21.65± 5.74	0.33±0.25	98.23±0.51	11.07±0.59	2.89±0.10	0.93±0.04
5	36.98±18.20	0.00±0.00	94.80±4.67	13.15±1.62	2.59±0.10	0.86±0.04
6	10.83[d]	0.00±0.00	99.50±0.50	#	3.37±0.15	0.92±0.02
8	27.79± 0.16	0.35±0.30	96.53±0.01	12.33±0.05	3.10±0.14	0.81±0.03
Mean	19.74±11.23	0.14±0.15	97.80±1.81	12.18±1.05	2.82±0.53	0.76±0.27

*: Mean±S.D.
a: Male sterility: both fertile and sterile pollen grains are few.
d: The value from one panicle; seed set percentage of the other panicles could not be investigated because of lodging by wind.
#: Weight of 100 kernels could not be measured because of a few number of seeds.

Table 4. Variation of five characters under cultivated condition in 1983.

Population No.	Plant length (cm)	Total dry weight (g)	Number		Total rhizome length (m)
			shoot	rhizome	
1	59.5± 3.6 (6.1)*	32.3±6.0 (18.6)	21.9±9.0 (41.1)	36.3±14.2 (39.1)	6.25±1.44 (23.0)
2	54.6± 2.7 (4.9)	28.7±3.4 (11.8)	23.8±2.1 (8.8)	41.9± 1.9 (4.5)	7.74±0.79 (10.2)
3	53.4± 3.6 (6.7)	24.8±3.8 (15.3)	17.7±1.1 (6.2)	29.3± 3.4 (11.6)	5.64±1.18 (20.9)
4	55.5± 8.8 (15.9)	22.1±8.4 (38.0)	13.7±4.5 (32.8)	26.0±10.9 (41.9)	4.47±2.23 (49.9)
5	66.5± 7.1 (10.7)	20.4±4.5 (22.1)	18.6±4.1 (22.0)	27.6± 7.3 (26.4)	4.81±0.78 (16.2)
6	56.1± 3.9 (7.0)	21.3±5.8 (27.2)	17.3±3.8 (22.0)	29.2± 6.2 (21.2)	5.21±1.56 (29.9)
7	53.0± 2.5 (4.7)	22.9±3.1 (13.5)	18.9±3.8 (20.1)	33.0± 8.7 (26.4)	4.98±1.05 (21.1)
8	64.0±12.6 (19.7)	23.2±6.0 (25.9)	18.1±6.1 (33.7)	26.7± 5.2 (19.5)	4.68±0.77 (16.5)
9	56.0± 4.0 (7.1)	21.0±4.8 (22.9)	15.8±1.5 (9.5)	28.3± 7.1 (25.1)	4.50±1.10 (24.4)
10	52.9± 9.3 (17.6)	22.2±2.8 (12.6)	17.0±7.6 (44.7)	29.6± 6.8 (23.0)	5.49±1.64 (29.9)
11	58.7± 5.1 (8.7)	23.2±2.6 (11.2)	16.3±2.5 (15.3)	30.2± 7.2 (23.8)	4.40±0.96 (21.8)
LSD					
0.01	13.3	9.3	8.2	14.3	2.23
0.05	9.9	6.9	6.2	10.7	1.67

* Mean±S.D. (C.V.)

obtained. Seed set percentages were very different among 11 populations and also in 3 years, 1982 to 1984, as shown in Table 5. The differences of seed set percentage which were observed among populations were generally larger than those among years. The seed set percentage of population No. 2 was extremely low in all three years.

The seed set percentage of each population under unbagged condition indicated 2.25 to 36.98%. The difference of seed set percentage among populations was smaller in cultivated condition than in the natural populations (Tables 3 and 5). Seed set percentage of population No. 2 in the cultivated condition indicated higher value, 17.72%, than that in the natural population.

The data of seed set percentage under bagged condition in natural population was obtained from only one population No. 3, 0.60±1.20% (not shown in Table 3), for almost all bags were blown away. In cultivated condition, the seed set percentage of each clone under bagged condition was very low, 0.00 to 0.35% (Table 3), as that of bagged panicles of population No. 3 in the field.

It was impossible to measure the 100 kernel weight of four populations (Nos. 1, 2, 6, and 8) in natural habitats because of a few number of seeds. In population No. 7, 100 kernel weight from only one panicle was measured, for the data from the other nine panicles could not be obtained

Table 5. Variation of seed set percentage, pollen fertility and 100 kernel weight in natural populations.

Population No.	Seed set percentage of three years (%) 1982	1983	1984	Mean	Pollen fertility (%) 1983	100 kernel weight (g) 1984
1	4.74± 4.85*	6.44±14.19	2.63± 0.34	4.60± 1.91	94.08±5.46	#
2	0.46± 0.89	0.10± 0.21	0.31± 0.30	0.29± 0.18	/[a]	#
3	7.89±13.86	12.82± 8.27	59.07±16.81	26.59±28.23	96.28±4.77	13.02±1.18
4	34.24±16.23	18.07± 7.37	51.96±20.42	34.76±16.95	97.64±2.17	15.71±2.31
5	-[b]	6.63± 5.35	34.09±22.46	20.36±19.42	94.86±9.36	12.99±2.38
6	38.53±15.86	17.78±15.71	4.07± 2.40	20.13±17.35	99.15±0.96	#
7	3.10± 2.84	7.81± 3.87	7.22± 2.53	6.04± 2.57	95.70±4.60	13.95[c]
8	2.02± 1.09	-[b]	7.98± 2.55	5.00± 4.21	95.68±2.92	#
9	-[b]	5.56± 6.50	39.88±15.67	22.72±24.27	98.21±2.21	14.14±1.36
10	-[b]	1.05± 0.64	14.33± 8.08	7.69± 9.39	97.67±1.66	8.69±0.63
11	-[b]	-[b]	26.73± 8.13	26.73	98.16±1.58	12.59±0.94
Mean	13.00±16.19	8.47± 6.51	22.57± 20.97		96.74±1.66	13.01±2.17

*: Mean±S.D.
b: Investigation could not be made, because of no panicle.
c: The value from one panicle: 100 kernel weight of the other nine panicles could not be measured because of a few number of seeds.
a and # are the same as in Table 3, respectively.

because of lack of the enough number of seeds for measurement. 100 kernel weight of population No. 10 indicated especially low value, 8.69 mg, compared with the other six populations which showed 12.59 to 15.71 mg, as shown in Table 5.

The 100 kernel weight in the cultivated condition was 11.07 to 13.15 mg (Table 3). There were not significant differences observed between field observation and cultivated condition in the 100 kernel weight.

DISCUSSION

The differences in the variability of morphological characters within population, as shown in I. cylindrica var. koenigii in this study were reported in Alopecurus aequalis Sobol. var. amurensis (Komar.) Ohwi (Matumura, 1967) and Arabidopsis thaliana (Linn.) Heynh. (Jones, 1971a, b). Matumura (1967) reported that the up-land type of A. aequalis var. amurensis had smaller seeds than low-land type and that the variance within population for seed length of up-land type collected in unstable habitat was apparently smaller than low-land type collected from more predictable environment. Jones (1971a, b) found that the plant height, rosette width, and flowering time of the

garden populations of A. thaliana, subject to gardening activities, were not variable within population but the disused railway track populations had a wide range of the plant height, rosette width, and of flowering time. The foredune population No. 2 of I. cylindrica var. koenigii had generally smaller variability of the plant length, total dry matter weight, total rhizome length, number of shoots and rhizomes within population than that of the other ten populations. The plants in foredune have suffered salt spray from the sea unpredictably. It is considered that the salt spray may have operated strong and unpredictable selection pressure in foredune. The low variability of the foredune population may be attributable to such selection pressure.

Ecotypic differentiation of weedy species in Japan was observed in Agropyron tsukushiense (Honda) Ohwi var. transiens (Hack.) Ohwi (Sakamoto, 1961, 1978), Alopecurus aequalis Sobol. var. amurensis (Komar.) Ohwi (Matumura, 1967), and Eleocharis kuroguwai Ohwi (Kobayashi and Ueki, 1979, 1983). In these three species, the relationships between ecotypic variation and the adaptation to each habitat were clarified.

In the morphological characters such as plant length, total dry matter weight, number of shoots and rhizomes, total rhizome length, and anther size of I. cylindrica var.

koenigii, significant differences were observed among populations (Tables 2, 3, and 4; Fig. 9).

In the roadside, abandoned field, orchard garden, and lawn, slashing has been conducted for many years; the frequency or method of slashing were different from one another. In addition, the plants in foredune have been exposed to the strong wind and salt spray. So these suggest that the populational differentiation in the morphology has been derived from both the founder effect and the different mode of selection pressure after establishment of the pioneer plants. The male sterile biotype observed in the Kii-Ohshima Island may be differentiated as a result of adaptation to foredune.

The wide differences were also detected in the seed set percentage. This differences may be attributable to population size and mostly to the density of the heading panicles in each population, for pollen fertility of the ten populations except population No. 2 was 94.08 to 99.15% (Table 5), and for this species is protandrous and anemophilous plant. Population No. 2 showed an extremely low seed set percentage. In this foredune population, both fertile and sterile pollen grains were very few but the morphology of pistil was normal. So it is considered that such a low value was due to male sterility.

Detailed study on the differentiation to foredune

biotype is going to be stated in the next Chapter 4.

Chapter 4. The differences between inland and foredune populations of *Imperata cylindrica* var. *koenigii* in the Kii Peninsula

INTRODUCTION

Though the genecological studies on weeds may be helpful to establish rational weed control programs as Kobayashi (1984) described, only a few such studies have been reported. The genecological studies on weeds in Japan were conducted on *Agropyron tsukushiense* (Honda) Ohwi var. *transiens* (Hack.) Ohwi (Sakamoto, 1961, 1978), *Alopecurus aequalis* Sobol. var. *amurensis* (Komar.) Ohwi (Matumura, 1967), and *Eleocharis kuroguwai* Ohwi (Kobayashi and Ueki, 1979, 1983), in which the relations between the intraspecific variation in the morphology and/or reproductive strategy and their adaptive mode to each habitat were discussed.

Matumura et al. (1980, 1983, 1984) reported the biotype of *Imperata cylindrica* (Linn.) Beauv. var. *koenigii* (Retz.) Durand et Schinz which had glabrous node, large caryopsis, and early flowering habit in the Nohbi Plain, Central Japan. Tominaga et al. (in preparation) found the

genetic differences among populations but not within population in the Kii-Ohshima Island.

In this study, the morphological differences between the inland and the foredune populations of I. cylindrica var. koenigii in the Kii Peninsula were clarified through the pot experiment. This species is protandrous and wind pollinated plant. The seed set percentage was investigated in natural population. On the basis of the differences in the plant size, morphology, and reproductive strategy between inland and foredune populations, the adaptive mode to each habitat was discussed.

MATERIALS and METHODS

Collection of clones

To clarify the morphological differences between the inland and the foredune populations, 17 and 16 populations were sampled from inland and foredune of the Kii Peninsula, respectively (Fig. 10). Five clones as apart as possible from one another in one population were collected by 1983. As shown in Table 6, clones of the inland populations were obtained in the abandoned fields, boundary of rice fields, orchard garden, rhododendron garden, and roadsides located in the mountainous regions which are remote more than 4.7

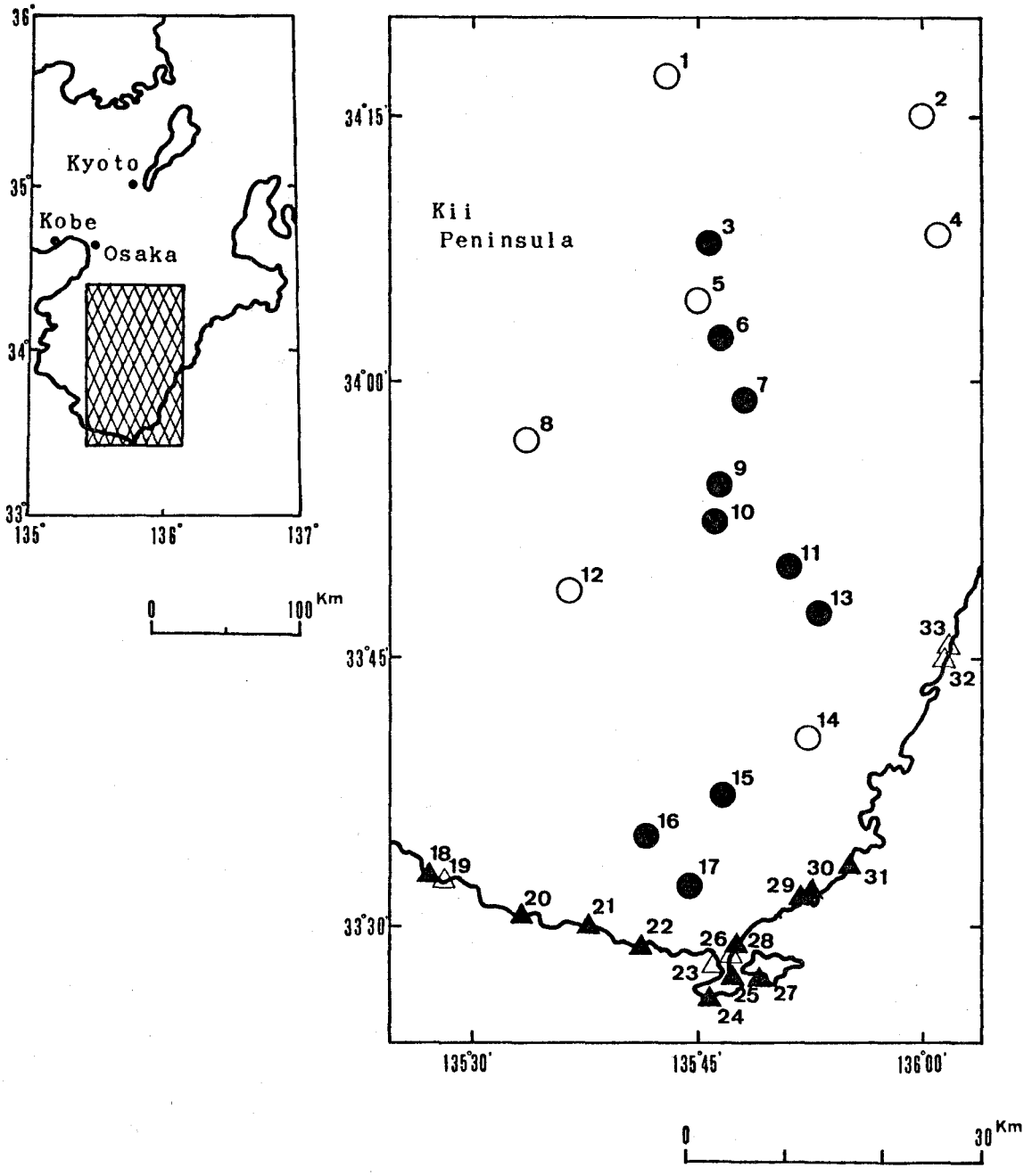

Fig. 10. Collection location of Imperata cylindrica var. koenigii

●,○: Inland population; ▲,△: Foredune population. Solid symbols indicate the populations of which seed set percentage in original habitat was investigated.

Table 6. The origin of clones investigated in this experiment.

<Inland populations>

Clone No.*	Locality			Distance from seashore	Habitat
	Latitude	Longitude	Altitude		
1	34°17'N	135°44'E	300 m	39.0 Km	Orchard garden
2	34 16	136 01	450	27.8	Roadside
3	34 08	135 46	375	40.8	Roadside
4	34 08	136 01	345	18.6	Boundary of rice field
5	34 05	135 46	310	38.2	Roadside
6	34 03	135 47	305	34.2	Roadside
7	34 00	135 48	195	30.4	Roadside
8	33 57	135 34	400	31.4	Abandoned field
9	33 55	135 47	175	27.8	Roadside
10	33 53	135 46	110	27.2	Abandoned field
11	33 50	135 51	45	18.0	Roadside
12	33 49	135 37	350	23.6	Roadside
13	33 48	135 53	35	13.4	Abandoned field
14	33 40	135 54	590	4.7	Rhododendron garden
15	33 37	135 47	115	13.0	Boundary of rice field
16	33 35	135 41	100	10.4	Roadside
17	33 32	135 45	15	6.0	Boundary of rice field

<Foredune populations>

Clone No.*	Locality			Distance from shoreline
	Latitude	Longitude	Altitude	
18	33°33'N	135°28'E	<5 m	<20 m
19	33 33	135 28	<2	<20
20	33 30	135 38	<3	<20
21	33 29	135 42	<5	<50
22	33 26	135 46	<3	<20
23	33 27	135 50	<1	< 3
24	33 27	135 50	<1	< 3
25	33 27	135 48	<2	<50
26	33 29	135 48	<3	<20
27	33 29	135 48	<2	<10
28	33 29	135 48	<2	<10
29	33 32	135 53	<2	<50
30	33 32	135 53	<2	<30
31	33 34	135 55	<3	<50
32	33 45	136 02	<5	<50
33	33 45	136 02	<5	<50

*: the same as in Fig. 10.

Km upcountry from the seashore. The clones from foredune populations were collected within 50 m from the shoreline, where they were exposed to salt spray from the sea. These clones were planted in the clay pots (20 cm diameter x 19 cm depth, about 6000 cm^3) individually at the Subtropical Plant Institute of Kyoto University (33°28'N, 135°50'E) in the Kii-Ohshima Island located at the southern extremity of the Kii Peninsula and the ramets from these clones were used in the following genecological studies.

Determination of number of clones per population

To determine the number of clones per population for the measurement of the morphological characters, the intra-populational variation in the plant length, total dry matter weight, and glume length of four inland (Nos. 1, 6, 10, and 15) and three foredune populations (Nos. 23, 28, and 33) was investigated preliminarily in 1983. At the experiment, five clones in one population, in total 35 clones were used.

The rhizomes of each clone were cut into about 10 cm long with 10 to 12 nodes on April 18th, 1983 and raised on the vermiculite bed in a greenhouse. Five ramets with shoot of 10 cm length per one clone, in total 175 ramets were transplanted in the clay pots (20 cm diameter x 19 cm depth, about 6000 cm^3) filled with clay loam on June 10th,

individually. Fertilizers, N 10, P 10, and K 10 Kg/10a, were basically applied. Plant length was measured on November 14th, and after that all ramets were dug up and dried up at 80 °C for 48 hours. Then dry matter was weighed individually. The length of ten glumes per clone planted in the clay pot was measured on June 27th.

Morphological differences between inland and foredune populations

Based on the results obtained in the above preliminary experiment, five ramets per clone and one clone per population were enough material number for assessing morphological differences between populations. At the experiment in 1984, to detect morphological differences between the inland and the foredune population, one clone was randomly selected in one population and five ramets per clone were planted as in the same way as the preliminary experiment in 1983. In total, 85 ramets from 17 clones in inland and 80 ramets from 16 clones in foredune populations were used for this pot experiment. Plant length, number of shoots and rhizomes, diameter and length of rhizome, dry matter weight of leaves, roots, and rhizomes of each ramet were individually investigated.

Pollen fertility, size of anther and glume

The pollen fertility, the length and width of anther and glume of 50 to 125 florets per one clone in cultivated condition were measured in the middle of May, 1984. The pollen fertility was observed by aceto-carmine staining. For these studies, six clones (Nos. 1, 2, 6, 10, 15, and 17) of inland and five clones (Nos. 21, 23, 28, 29, and 33) of foredune populations, which were planted in the clay pots by 1983, were used. The pollen fertility, the size of anther and glume were also investigated in the original habitat.

Seed set percentage in natural population

The seed set percentages of five panicles per one population in the original habitat were investigated in late June, 1984. This investigation was conducted at the 10 inland and 11 foredune populations of the Kii Peninsula (Fig. 10).

RESULTS

Determination of number of clones per population

After the experiment, significant differences in plant length, total dry matter weight, and glume length were detected among populations, but were not observed within population (Table 7). This result was consistent with that obtained in the 11 populations of the Kii-Ohshima Island (Chapter 3).

Morphological differences between inland and foredune populations

The significant differences between the inland and the foredune populations were observed in five morphological characters (Fig. 11). The clones from inland populations were longer in plant length, heavier in leaf, rhizome, and total dry matter weight, and larger in the diameter of rhizome than those of foredune populations. The mean number of shoots and rhizomes, and total rhizome length of clones from inland populations were smaller than those obtained in foredune populations (Fig. 11).

Table 7. Analysis of variance for three characters in preexperiment in 1983.

Source of variation	D.f.	Meansquares		
		Plant length	Total dry weight	Glume length
Among populations	6	113.89 **	99.86 **	0.755 **
Within population	4	30.77	14.67	0.012
Error	24	17.47	22.12	0.101

**: significant at 1% level.

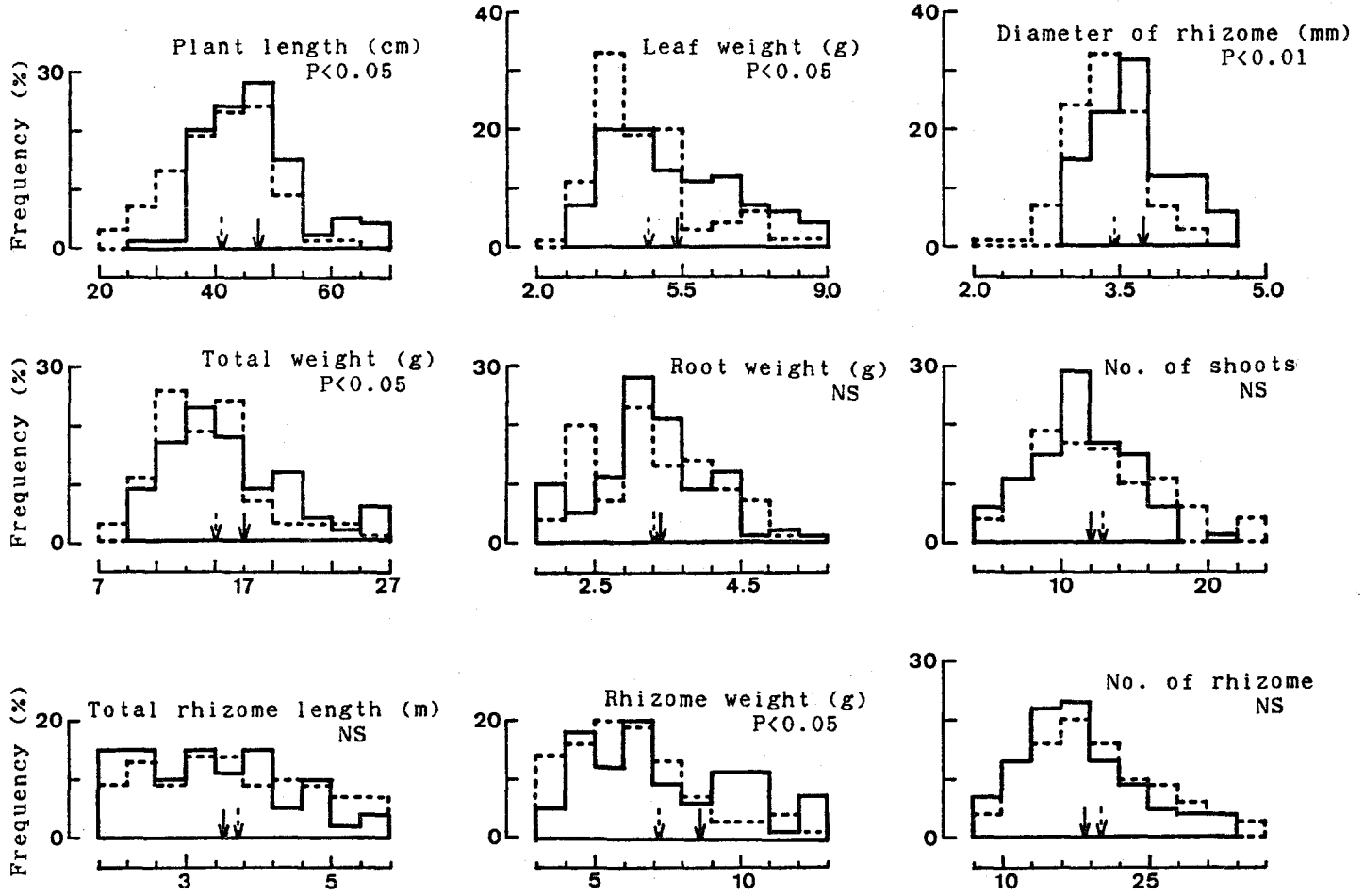

Fig. 11. Differences in nine characters between inland and foredune populations.

———: Inland populations; -----: Foredune populations.
NS: not significant. Arrow indicates the mean.

Pollen fertility, size of anther and glume

The pollen fertilities of the clones from inland populations were 94.80 to 99.83%, but the pollen grains of foredune populations were scarcely found out without exception.

The size of anther and glume was very stable. The significant differences between the original habitats and the cultivated condition were not observed (Table 8) and no wide variation was found within population (Fig. 12). As shown in Fig. 12, the anthers of the clones from foredune populations were very small and had few pollen grains, though the morphology of the pistil was normal as those of inland populations. The glume of foredune populations was statistically longer than that of the inland populations, as observed in the natural populations.

Seed set percentage in natural population

As shown in Table 9, the seed set percentages of ten inland populations exhibited wide variation, 4.26 to 73.31%. Those of the 11 foredune populations ranged 0.18 to 3.60%. The six populations among them showed less than 1.00%.

Table 8. The results of T-test for the size of anther and glume in original habitats and cultivated condition.

	Anther		Glume
	length	width	length
Original habitats	2.82±0.53 *	0.76±0.27	3.70±0.33
Cultivated condition	2.55±0.50	0.75±0.25	3.63±0.42
T-value	1.32 (NS)	0.42 (NS)	0.46 (NS)

*: Mean±S.D. (mm).
NS: not significant.

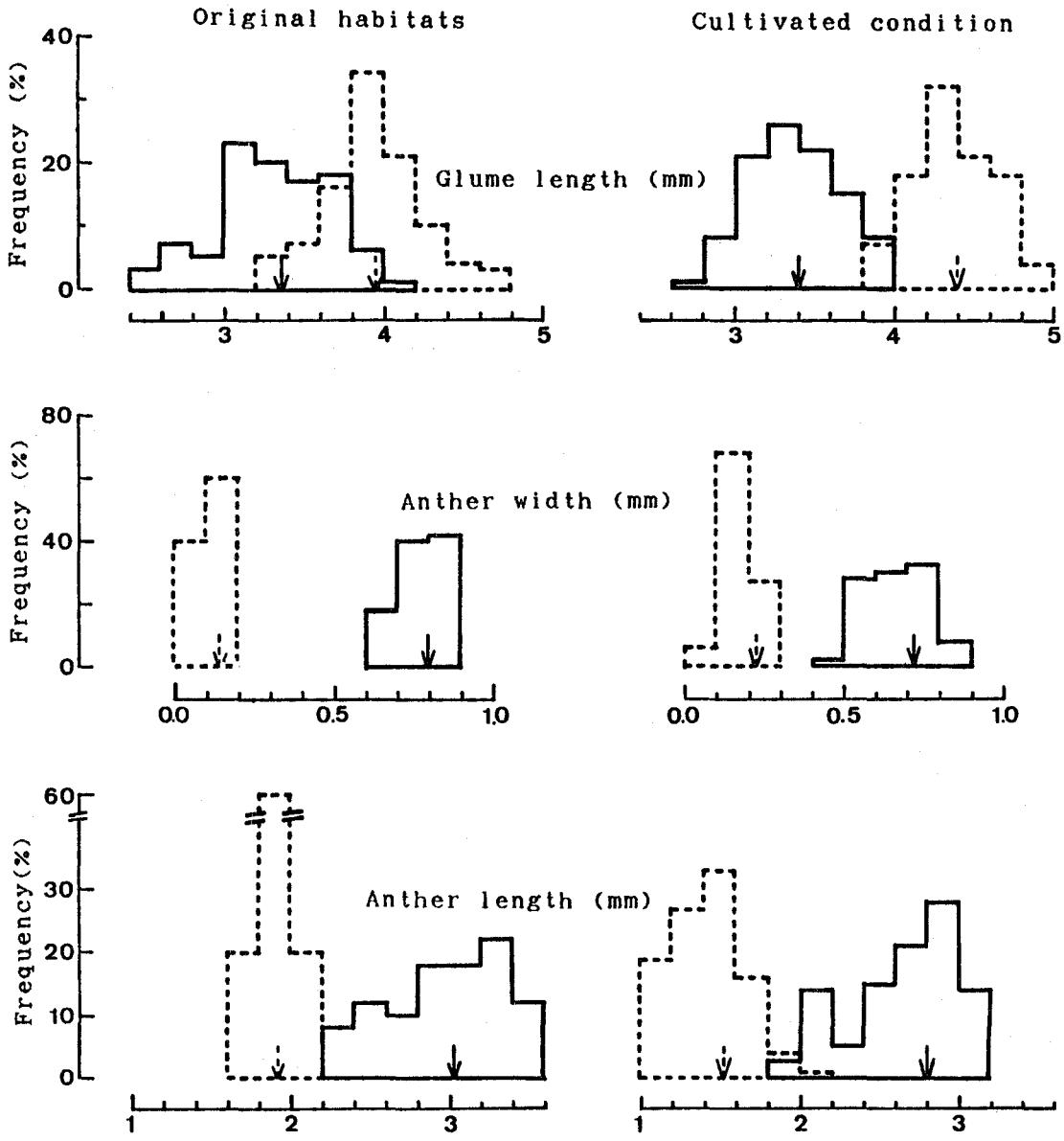

Fig. 12. Anther size and glume length in original habitat (Left) and cultivated condition (Right).

———: Inland populations, -----: Foredune populations. These three characters were significantly different at the 1% level between the two populations. Arrow indicates the mean.

Table 9. Variation of seed set percentage in original habitats.

Population	Number of populations								Mean	Range	
	Seed set percentage (%)										
	0	5	10	20	40	60	80	Total	Mean ± S.D.	Max.	Min.
Inland	1	1	2	2	1	3		10	34.90±26.77	73.31	4.26
Foredune	11							11	1.14± 1.14	3.60	0.18

DISCUSSION

The clones from foredune populations were male sterile and had shorter plant length with longer glume compared with those from inland populations. They also had slenderer rhizomes (Fig. 11).

The clones in foredune have been exposed to the stiff sea breezes accompanying with the movement of sand and have coexisted with a few number of species. It is presumable that the small plant type of foredune populations with long, many rhizomes is adapted to the stiff sea breezes and the movement of sand. Those characteristics were very resemble to Agrostis stolonifera Linn. of maritime habitats being a small compact tufted plant with many short stolons (Aston and Bradshaw, 1966). Another resemble result in Hypericum perforatum Linn. was also reported by Pritchard (1960).

In inland populations, man's impact, especially slashing has been made frequently over many years. Furthermore, this weed species of the inland populations has competed with many other species. The larger plant type of inland populations may be advantageous for competing with the other species and also their thick rhizome with abundant reserve substances for the quick regrowth after slashing.

Actually, in the abandoned fields or roadsides of the southwestern parts of Japan, where slashing has been conducted several times a year, I. cylindrica var. koenigii grew densely and was dominant as described in the abandoned field of the Kii-Ohshima Island in Chapter 2.

The wide variation in seed set percentage among ten inland populations (Table 9) was attributed to the density of the flowering panicles and population size, because this species is protandrous and wind-pollinated plant. On the other hand, the seed set percentages of 11 foredune populations were extremely low. These low values are attributable to male sterility, for their anthers were empty, although the morphology of pistil was normal. The reproduction of foredune population was made asexually through rhizomes. The descendants of the same genotype with parent may be advantageous to establish under such unstable habitat.

The differences in salt tolerance between inland and foredune populations were clarified in another study (Tominaga, unpublished). The decrease in dry matter production of clones from foredune populations under salt application was smaller than those from inland populations. Such differentiation in salt tolerance has already reported in Festuca rubra Linn. (Lane and Lyon, 1966) and Typha domingensis Pers. (McNaughton, 1966).

The genetic differences between inland and foredune populations detected in this experiment may be resulted from the different kinds of selection pressures, such as salt tolerance proposed in this study.

Chapter 5. Geographical variation of *Imperata cylindrica* in Japan

INTRODUCTION

The harmful upland perennial weed, *Imperata cylindrica* (Linn.) Beauv. is widely distributed in the subarctic to subtropical zones in Japan from Hokkaido to Okinawa Prefecture. *I. cylindrica* in Japan is classified into two varieties based on the presence or absence of the hairs on node of culm. *I. cylindrica* var. *koenigii* (Retz.) Durand et Schinz is hairy. Conversely var. *genuina* Durand et Schinz is glabrous. Furthermore, var. *genuina* is divided into two forms: *I. cylindrica* var. *genuina* form. *pallida* Honda has light green leaf sheath, whitish brown stigma, and slender plant type; form. *typica* Honda has reddish purple leaf sheath and stigma (Honda, 1930).

The plant species which are distributed widely over the wide latitudes from north to south regions have generally geographical variations adapted to the temperature, photoperiod, or other climatic factors in their habitat. There were some reports on the latitudinal cline of weed species in Japan. In *Echinochloa oryzicola* Vasing., the

strains from northern parts of Japan headed earlier than those from southern parts except some cases (Yabuno, 1966) and the latitudinal cline of Plantago asiatica Linn. in the phenology and growth of seedlings was recognized (Yamanishi and Fukunaga, 1983). As for I. cylindrica, Tominaga et al. (1986) reported the latitudinal cline in plant length, total dry matter weight, and phenology such as emergence, heading, and death of aerial parts.

In order to elucidate the geographical variation in the morphology, phenology, plant size, and heading response of I. cylindrica in Japan to temperature or photoperiod, the genecological studies were made at the Subtropical Plant Institute of Kyoto University in the Kii-Ohshima Island. The differentiation to some local populations was also clarified based on the results of principal component analysis (PCA). The relationships between the geographical variation and distribution were discussed.

MATERIALS and METHODS

Latitudinal variation in the morphology, phenology, and plant size

From Hokkaido to Okinawa Prefecture, 388 clones of I. cylindrica (Fig. 13) were collected from the coastal sandy beach, roadside, boundary of the rice or upland field, lawn, abandoned field, and bank along aqueduct by 1983. These clones were maintained individually at the Subtropical Plant Institute of Kyoto University.

Fifty-two clones out of 388 clones (Fig. 13) were selected to clarify the variation in the dry matter production. Their original habitat and annual mean temperature were shown in Table 10. The annual mean temperature of original habitat was calculated according to Masaki (1967).

The rhizomes of 52 clones were dug up on April 16th, 1985. Five ramets per one clone, in total 260 ramets were raised and transplanted in the clay pots (20 cm diameter x 19 cm depth, about 6000 cm^3) individually on May 28th, 1985. Fertilizers, N 10, P 10, and K 10 Kg/10a were basically applied. All ramets were dug up in early November, 1985 and plant length, number of shoots and rhizomes were investigated. The plants were separated into leaves, rhizomes and roots, and dried up at 80 °C for 48 hours. The dry matter weight of each organ was measured individually.

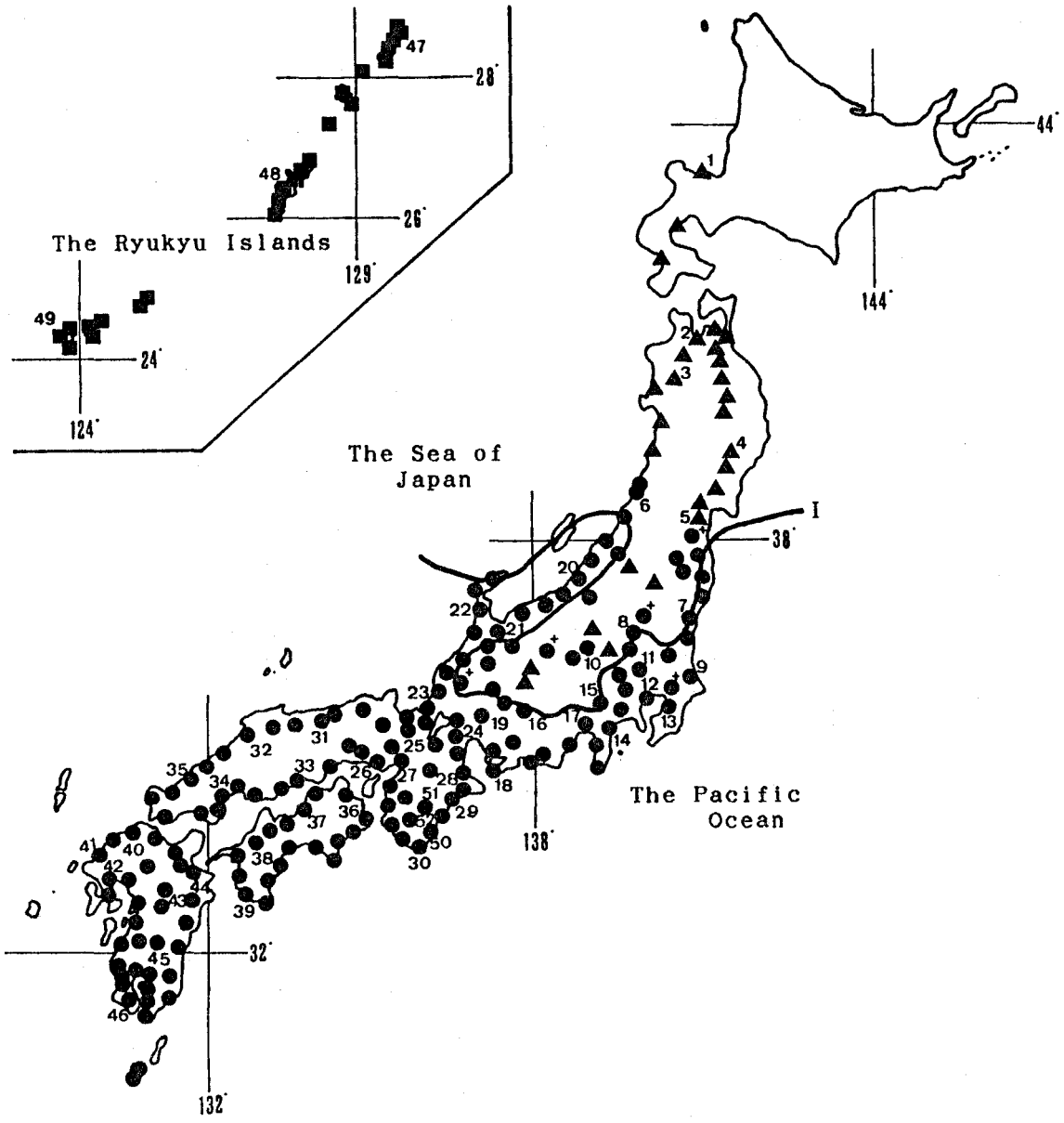

Fig. 13. Distribution of Imperata cylindrica var. koenigii (●, ■) and var. genuina (▲) in Japan.

Symbol with number shows the clone which was investigated dry matter production and heading response. The numbers are the same as in Table 10.
●⁺: the clone which headed in autumn; ■: the evergreen clone.
Line I indicates the boundary between the summer green broad leaved forest zone and the evergreen broad leaved forest zone (from Miyawaki, 1977).

Table 10. Origin and habitat of clones investigated their dry matter production and heading response.

Clone No.	Locality			Annual mean temperature*	Habitat
	Latitude	Longitude	Altitude		
1	43°12'N	140°50'E	5 m	7.2°C	Coastal sandy beach
2	40 47	140 38	50	9.4	Roadside
3	40 15	140 22	32	10.0	Roadside
4	39 28	141 08	88	10.6	Roadside
5	38 22	140 53	50	11.9	Boundary of rice field
6	38 59	139 51	13	11.4	Roadside
7	36 58	140 52	25	13.5	Roadside
8	37 01	139 44	700	9.4	Roadside
9	36 10	140 36	51	14.1	Roadside
10	36 17	138 55	150	13.2	Roadside
11	36 04	139 25	25	14.2	Roadside
12	35 45	139 21	125	14.0	Lawn
13	35 42	140 15	25	14.7	Roadside
14	35 37	139 09	300	13.1	Roadside
15	35 32	138 53	500	12.0	Railwayside
16	35 21	137 48	600	11.5	Boundary of upland field
17	34 45	137 57	40	15.3	Roadside
18	34 35	137 02	30	15.4	Roadside
19	35 23	136 42	13	14.7	Boundary of rice field
20	37 28	138 50	25	12.7	Roadside
21	36 40	136 59	35	13.2	Bank along aqueduct
22	37 03	136 44	15	12.9	Boundary of rice field
23	35 41	136 05	75	13.9	Boundary of upland field
24	35 21	136 18	100	14.1	Boundary of rice field
25	35 29	135 28	100	13.9	Boundary of rice field
26	34 50	134 25	50	14.7	Vacant land
27	34 48	135 33	50	14.9	Bank along railway
28	33 58	135 48	163	15.1	Roadside
29	34 03	136 12	60	15.7	Boundary of upland field
30	33 27	135 50	50	16.3	Abandoned field
31	35 34	134 19	50	13.9	Boundary of rice field
32	35 17	132 37	25	14.2	Vacant land
33	34 32	133 37	50	14.9	Vacant land
34	34 17	132 16	50	15.0	Roadside
35	34 37	131 37	50	14.6	Roadside
36	34 00	134 36	5	15.8	Roadside
37	34 06	133 40	29	15.5	Boundary of rice field
38	33 48	132 51	100	15.3	Roadside
39	32 43	133 01	100	16.4	Edge of parking zone
40	33 47	130 33	50	15.3	Roadside
41	33 13	130 05	50	15.8	Vacant land
42	33 03	129 50	50	16.0	Roadside
43	33 09	131 03	450	13.7	Boundary of rice field
44	33 04	131 38	100	15.9	Roadside
45	32 31	131 11	500	14.1	Roadside
46	31 14	130 38	40	18.0	Roadside
47	28 25	129 38	10	20.9	Roadside
48	26 26	127 47	50	22.5	Roadside
49	24 21	123 45	50	24.1	Roadside
50	33 45	136 02	5	16.3	Coastal sandy beach
51	34 00	135 48	195	14.9	Roadside
52	33 55	135 47	175	15.1	Roadside

*: Annual mean temperature (T) was calculated by the multiple regression equation from Masaki (1967), $T=33.4-1.03X_N+0.13X_E-0.0057X_A$, where, X_N, X_E, and X_A show latitude, longitude, and altitude, respectively.

Principal component analysis (PCA) based on the correlation matrix of ten characters was practiced using 47 clones from Honshu, Shikoku, and Kyushu District (Fig. 13) except five clones. As two clones, one from Hokkaido (Clone No. 1) and the other from Akita Prefecture (No. 3), did not produced panicle, the period to heading could not be obtained. Three clones, one from the Amami-Ohshima Island (No. 47) and two from the Ryukyu Islands (Nos. 48 and 49) continued their growth even in winter and such evergreen habit could not be assessed in this study.

The ten characters analyzed were as follows: Plant length (X_1), total dry matter weight (X_2), number of shoots (X_3) and rhizomes (X_4), total rhizome length (X_5), the dry matter partitioning ratio to rhizome (X_6), days to the first emergence of the new shoot (X_7), to heading of panicle (X_8), and to death of all aerial parts (X_9) after transplanting, and the days from emergence to death of aerial part (X_{10}). X_1, X_2, X_3, X_4, X_5, and X_6 were measured at early November, 1985. The data of dry matter partitioning ratio to rhizome (X_6) were transformed into arcsin $\sqrt{\text{percentage}}$ for statistical treatment.

Clonal variation in the effects of temperature or photoperiod on heading

To clarify the relationships between the distribution

and the heading response to temperature or photoperiod of I. cylindrica, the effects of temperature or day-length on the heading of 52 clones (Fig. 13) were investigated. In each experimental plot, three ramets per one clone, in total 936 ramets (3 ramets x 52 clones x 6 experimental plots) were used. The rhizomes of each clone in the clay pot were dug up on April 13th, 1984 and they were cut into about 10 cm long with 10 to 12 nodes and raised on vermiculite beds in a greenhouse. On June 8th, 1984, eighteen ramets with 10 cm plant length per one clone were transplanted in the clay pots (20 cm diameter x 19 cm depth, about 6000 cm^3) filled with clay loam individually as in the same way as the pot experiment on the dry matter production. After that, those ramets had been raised at the experimental field of the Subtropical Plant Institute under the natural condition until the beginning of the photoperiodic or temperature treatment. The treatments had been conducted from October 1st, 1985 to June 30th, 1986 as follows: Temperature experiment was composed of three plots, high temperature plot (mean temperature; 17.7 ℃), medium temperature plot (14.6 ℃), and low temperature plot (13.0 ℃). Photoperiodic experiment consisted of three regimes, long day treatment (16 hours day length), natural day length, and short day treatment (8 hours day length). In long day treatment plot, 75 W incandescent lamps for

illumination culture were used from 4:00 to 20:00. The lamps were set 50 cm above the tips of plants and at plant level the minimum reading of 500 lux was obtained. Short day treatment was conducted by covering the ventilated frame (2.0 m width x 8.5 m length x 1.8 m height) with opaque sheets from 17:00 to 9:00. In the course of the experiment, the heading date was investigated for 3 to 13 panicles per one ramet. The heading date was defined when the tip of panicle emerged from the leaf sheath of flag leaf.

RESULTS

Clinal variation in the morphology, phenology, and plant size

On the basis of the presence, I. cylindrica var. koenigii, or absence, var. genuina, of hairs on node of culm, the collected 388 clones were divided into two varieties clearly. As shown in Fig. 13, I. cylindrica var. koenigii was distributed in the southern parts of the Tohoku District and southwards, while, var. genuina was in Hokkaido, northern parts of the Tohoku District and highland regions of Fukushima, Gunma, and Nagano Prefecture. Var. koenigii headed in May and showed the wide variation

in the heading time. Conversely var. genuina headed especially early in April but all clones from Hokkaido and some from the northern parts of Tohoku District did not head in the Kii-Ohshima Island. Var. genuina was shorter in plant length and had waxy glaucous leaf sheath, but var. koenigii did not have ones.

This species generally heads once a year in May but its heading is sometimes observed in summer or autumn in the natural population where the aerial parts of this weed were cut. But in this experiment without cutting, five clones from Yamamoto-cho (Miyagi Prefecture), Fujiwara-cho (Tochigi Prefecture), Sakura-city (Chiba Prefecture), Saku-city (Nagano Prefecture), and Imajo-cho (Fukui Prefecture) of var. koenigii (Fig. 13) headed in autumn, September to October constantly. However, any relations were not found between the distribution of those five clones and ecological factors of their original habitats.

The significant relationships were observed between the latitude or annual mean temperature of the original habitat and phenology or plant size. The days from transplanting to the first emergence of the new shoot increased significantly with the increase of the latitude of original habitat and they were also observed to increase with the decrease of the annual mean temperature (Fig. 14). The heading date (Fig. 15) and death time of aerial part (Fig.

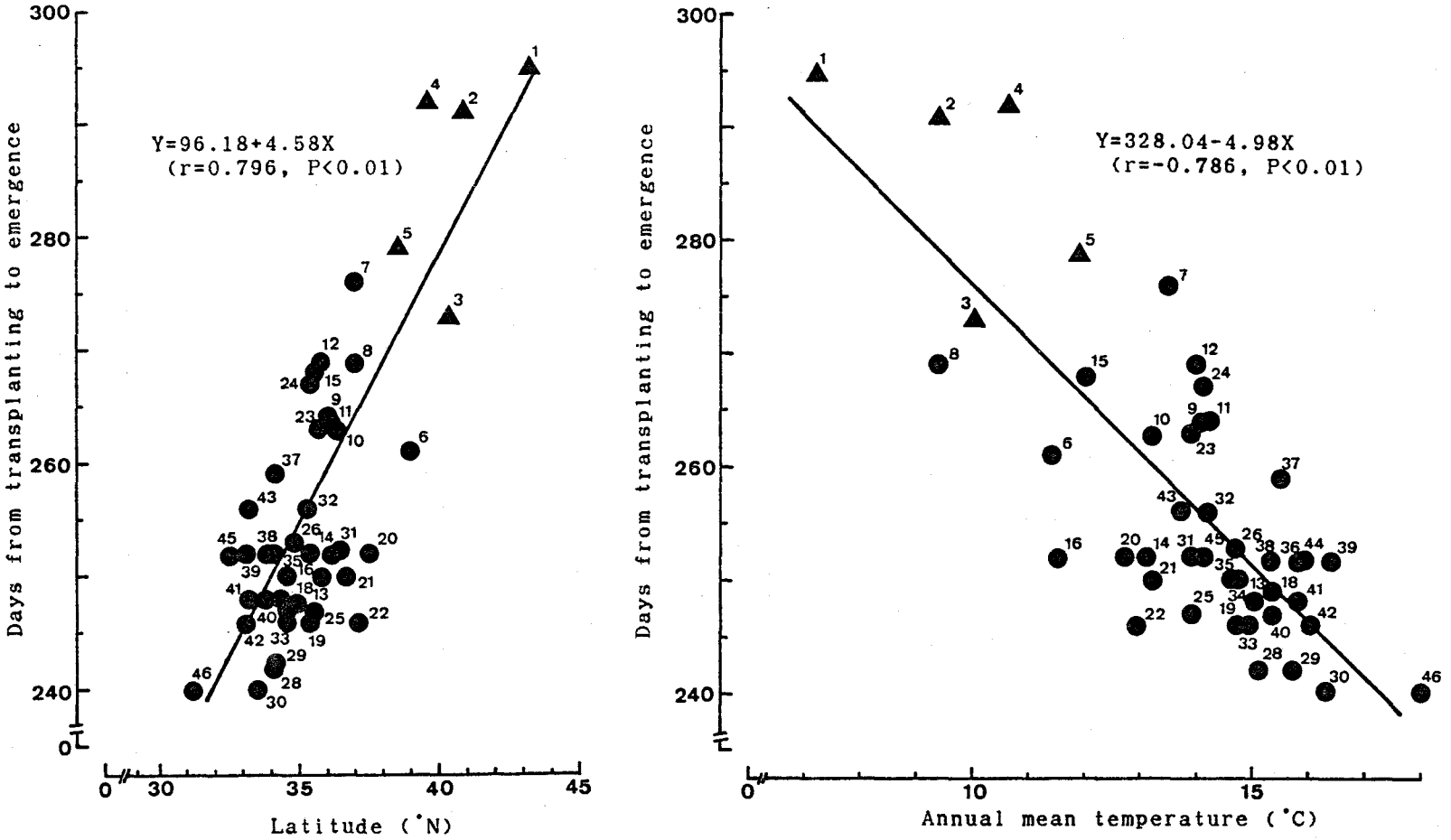

Fig. 14. Clinal variation in emergence date of Imperata cylindrica in Japan.

Symbols and numbers are the same as in Table 10 and Fig. 13.

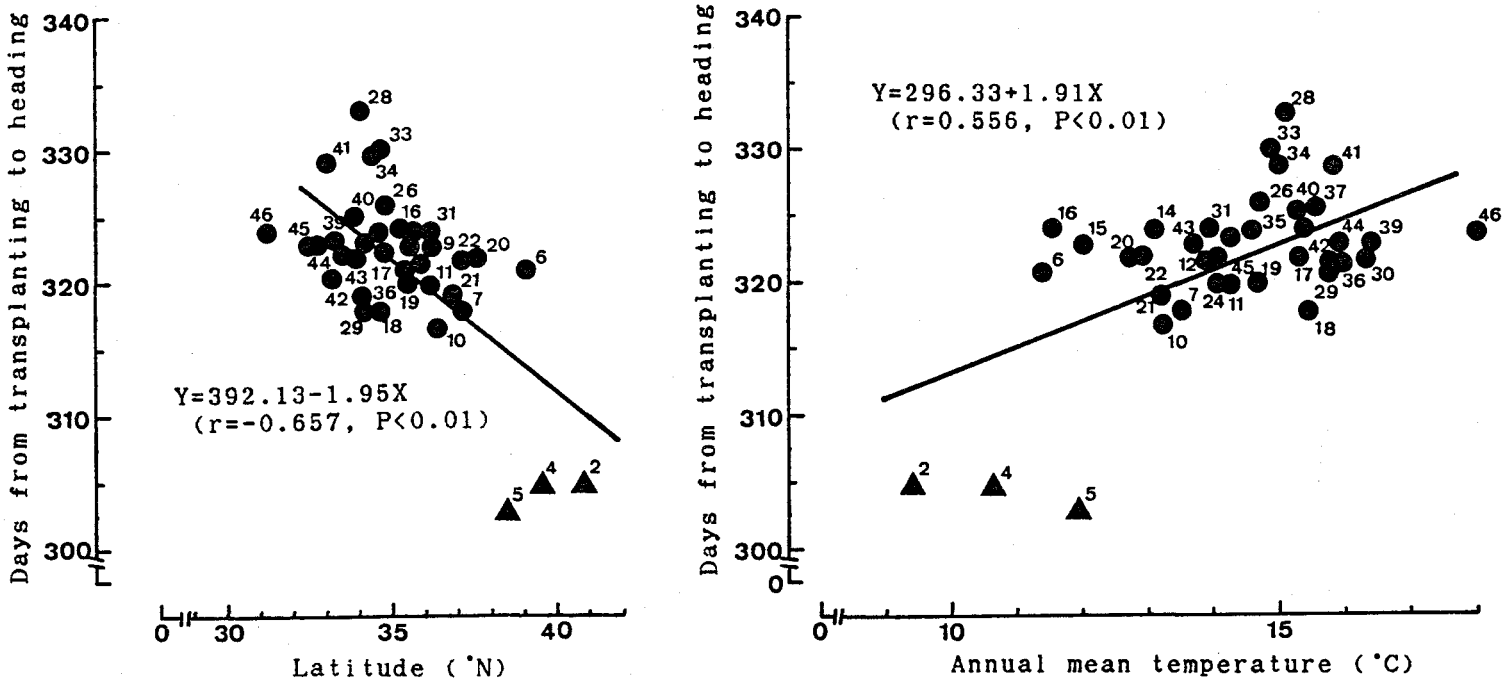

Fig. 15. Variation in heading date of Imperata cylindrica in Japan.

Symbols and numbers are the same as in Table 10 and Fig. 13.
Clones No. 1 and 3 which did not head during observation were not shown.

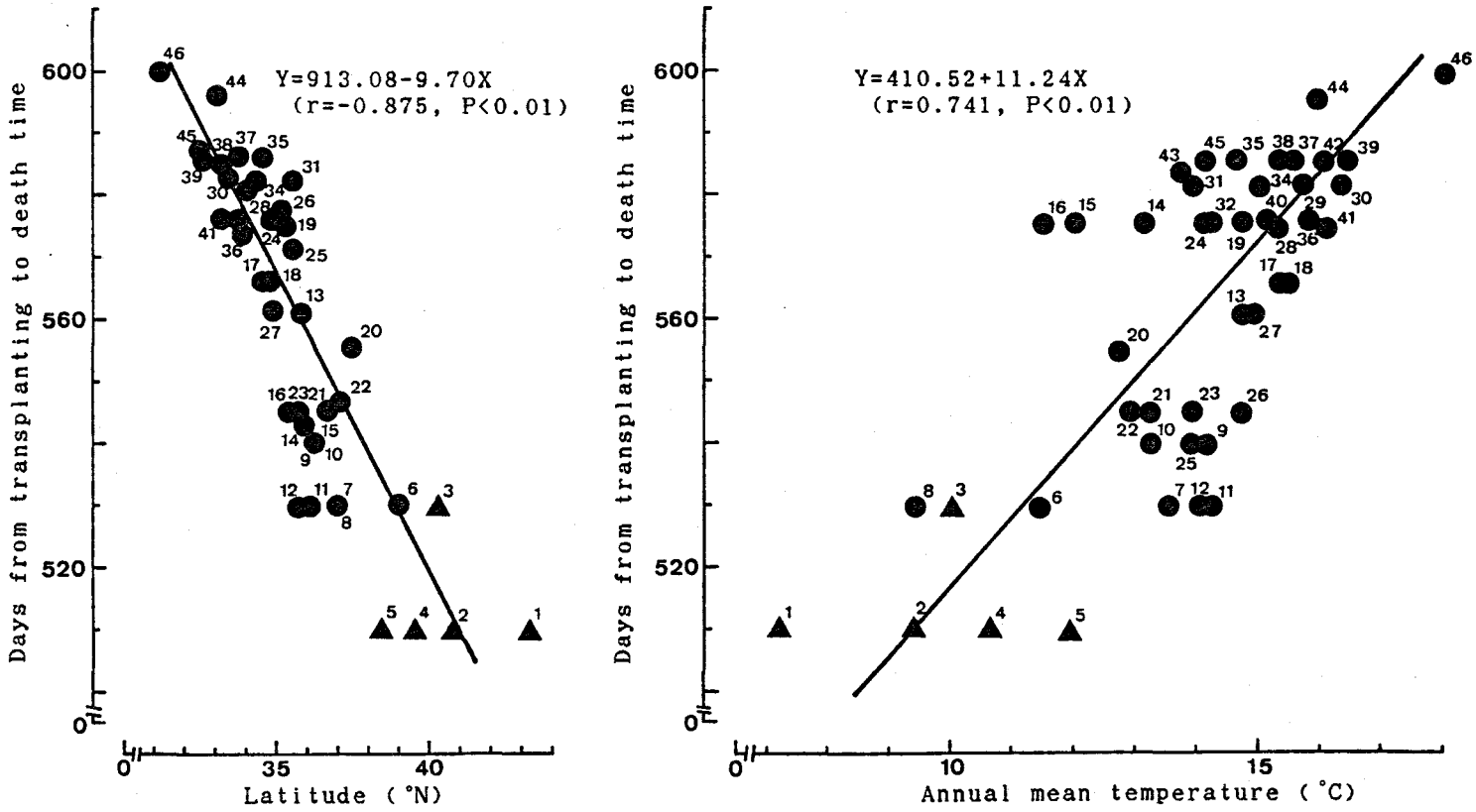

Fig. 16. Clinal variation in death time of aerial parts of Imperata cylindrica in Japan.

Symbols and numbers are the same as in Table 10 and Fig. 13. Clones No. 47, 48, and 49 were evergreen.

16) related negatively to the latitude of the original habitat and positively to the annual mean temperature. Var. genuina headed exceptionally early but two clones, one from Hokkaido (No. 1) and the other from Akita Prefecture (No. 3) were not observed to head during this experiment. Most panicles of three clones, one from Amami-Ohshima Island (No. 47) and the others from the Ryukyu Islands (Nos. 48 and 49), were produced in mid-May, but the production of some panicles was observed intermittently until October. In the natural population of those three clones, heading was observed even in winter. The days from emergence to death of aerial parts of this weed were negatively associated with the latitude and positively with the annual mean temperature of the original habitat (Figs. 17 and 18). Three clones, one from Amami-Ohshima Island (No. 47) and two from the Ryukyu Islands (Nos. 48 and 49) continued their growth even in winter but the other clones stopped growing and entered dormant state. The plant length (Fig. 19) and total dry matter weight (Fig. 20) were found to have some significant relation with the latitude of original habitat, negatively.

As shown in Table 11, the correlation matrix of the ten characters of 47 clones was computed. The factor loading, eigen value, and contribution were shown in Table 12. The contributions of the first, second, and the third

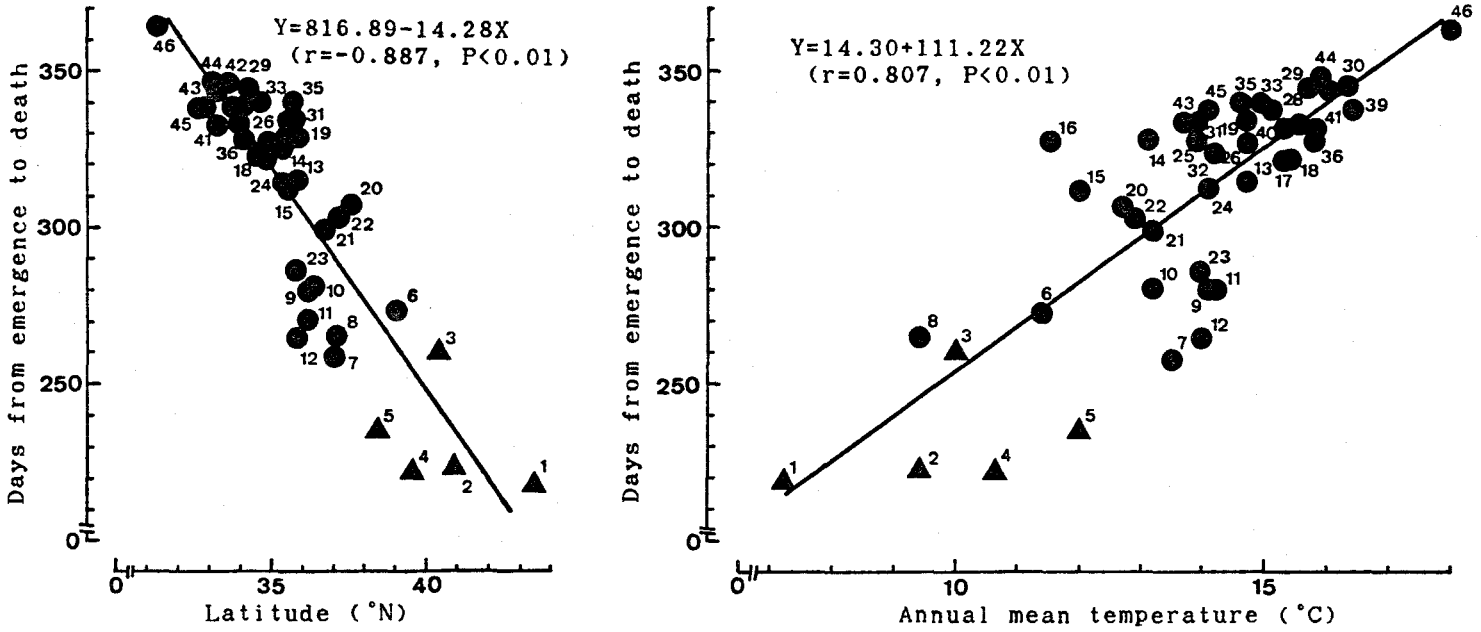

Fig. 17. Clinal variation in the days from emergence to death of aerial parts of Imperata cylindrica in Japan.

Symbols and numbers are the same as in Table 10 and Fig. 13.

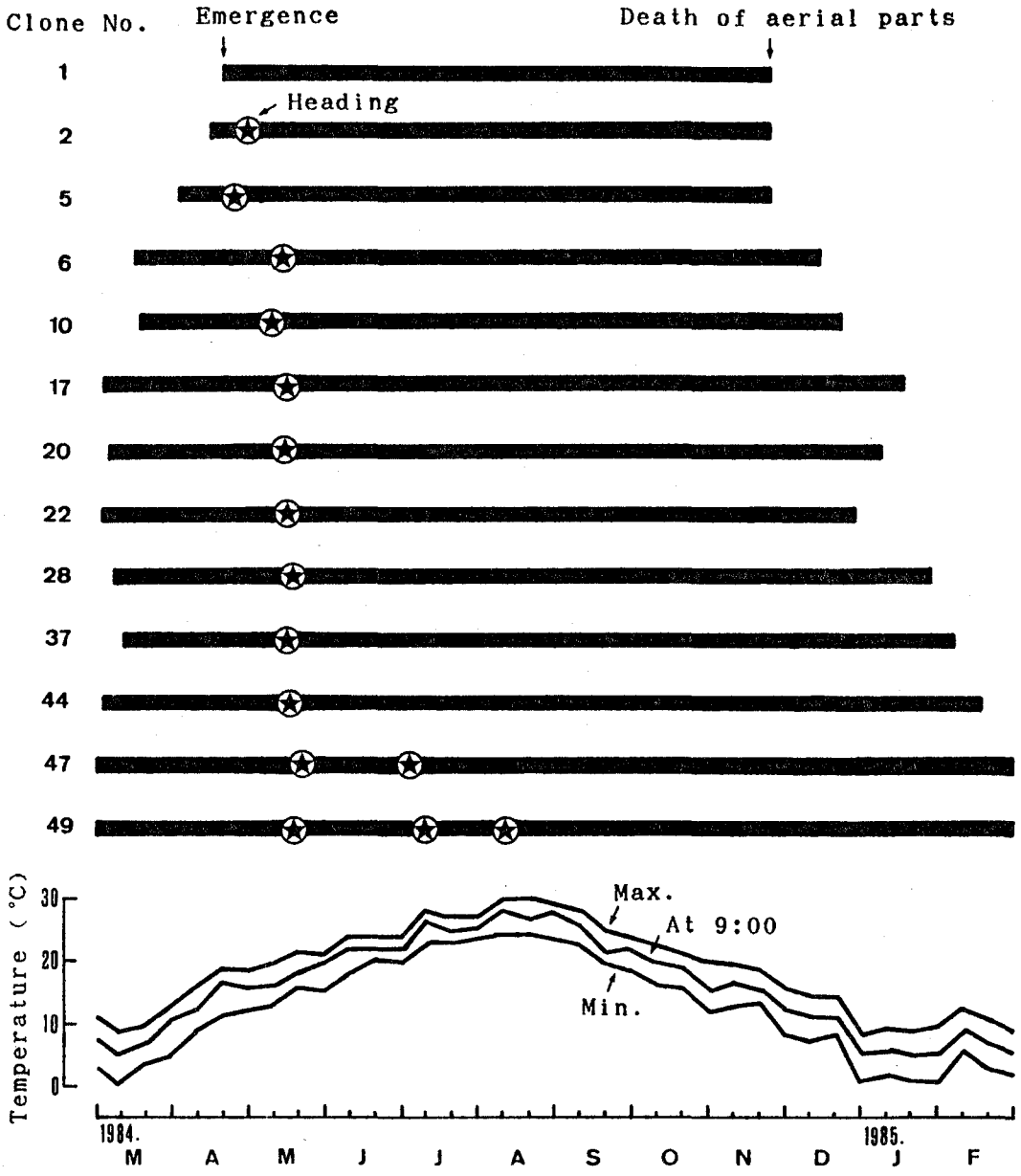

Fig. 18. Phenology of 13 clones of Imperata cylindrica and changes of temperature in the experimental field of the Kii-Ohshima Island.

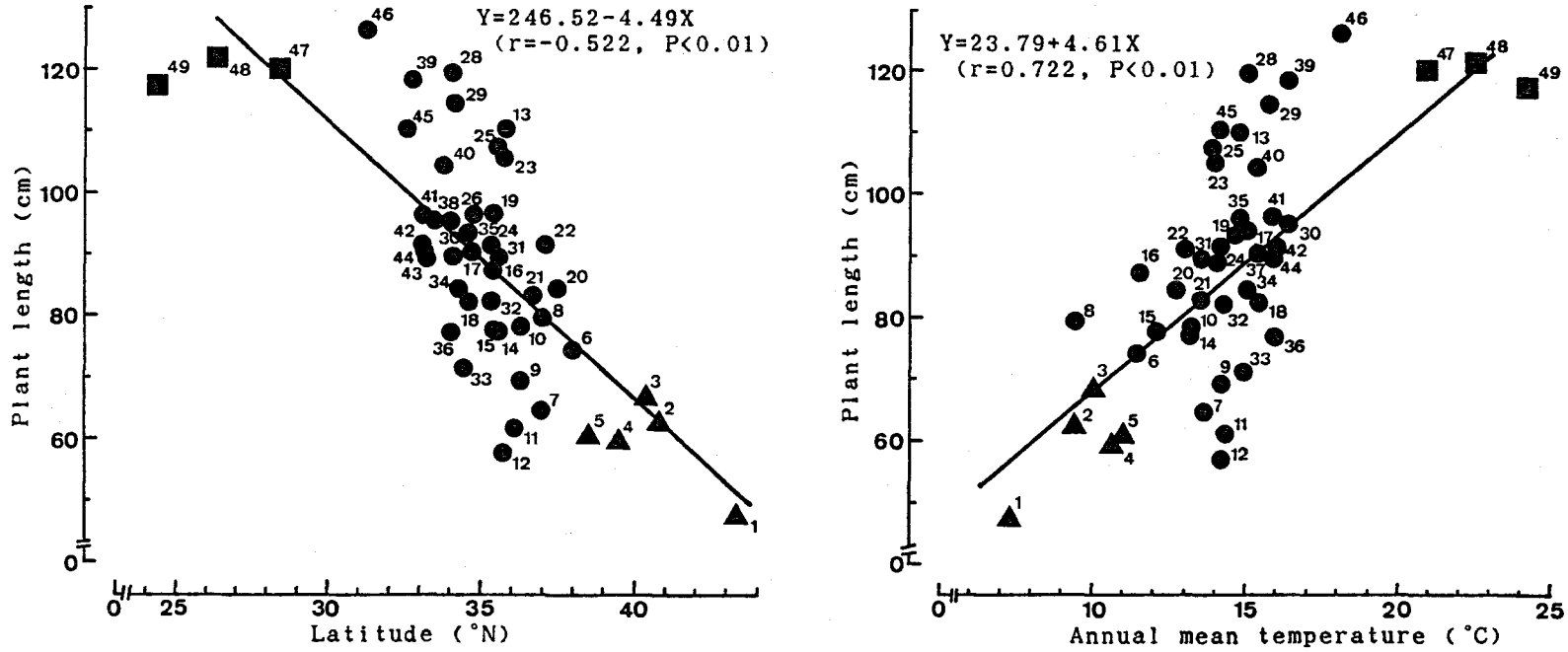

Fig. 19. Clinal variation in plant length of Imperata cylindrica in Japan.

Symbols and numbers are the same as in Table 10 and Fig. 13.

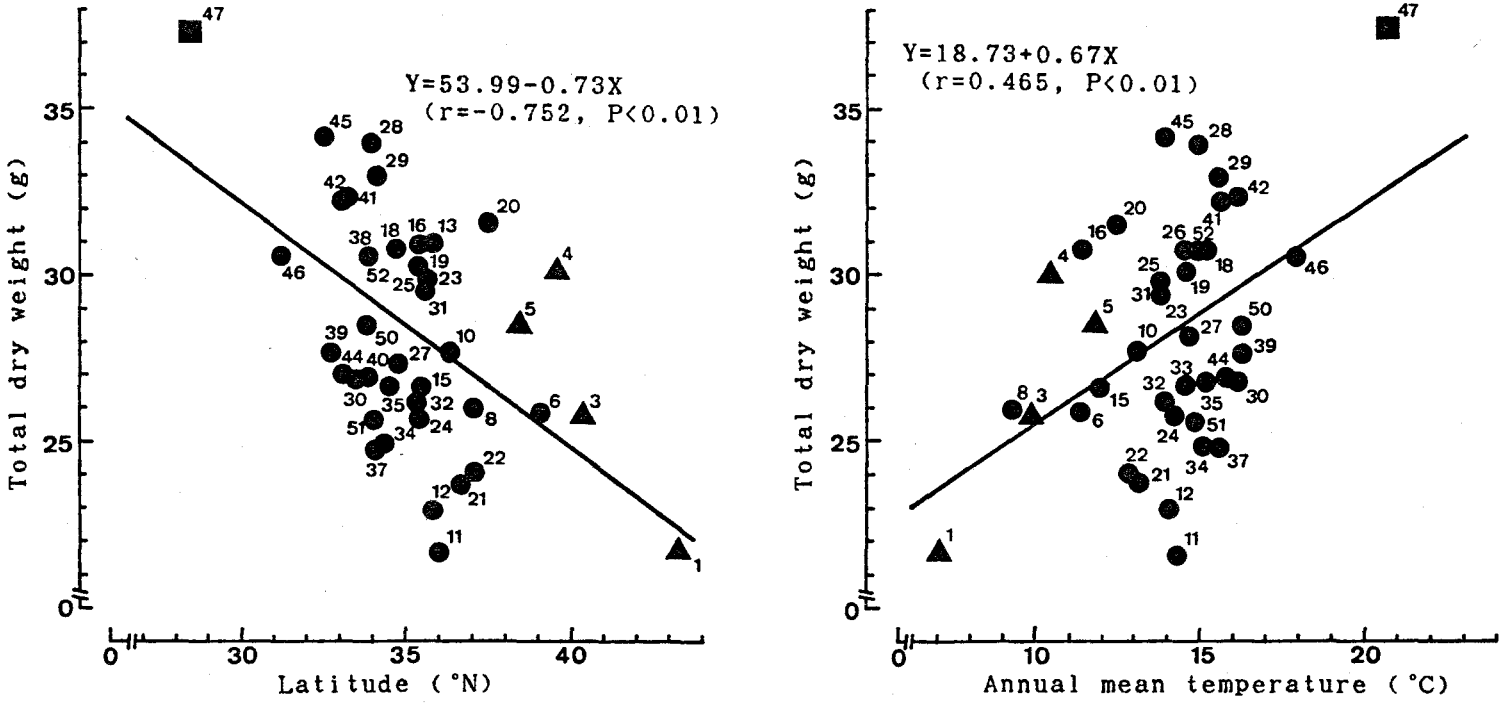

Fig. 20. Clinal variation in total dry weight of Imperata cylindrica in Japan.

Symbols and numbers are the same as in Table 10 and Fig. 13.

component were 43.7, 28.1, and 12.5%, respectively, and accumulative contribution from the first to the third component reached 84.4%. Based on the value of the factor loading of the ten characters, it may be explained that the first principal component (Z_1) shows plant length and phenology, the second one (Z_2) expresses rhizome length and number, and the third (Z_3) indicates the dry matter partitioning ratio to rhizome. Z_1 value increased with the increase of plant length, days from transplanting to heading, days to death time of aerial parts, and days from emergence to death, but with the decrease of days to emergence. Z_2 value increased with the increase of rhizome length and number; Z_3 value increased with the increase of the dry matter partitioning ratio to rhizome.

Based on the results of principal component analysis (PCA), 47 clones were clearly divided into three groups as shown in Fig. 21, A; clones of I. cylindrica var. genuina from the northern parts of the Tohoku District, B; clones of var. koenigii from the southern parts of the Tohoku to northern parts of the Kyushu District, and C; clones of var. koenigii from the southern parts of the Kyushu District. Var. genuina collected from the northern parts of Tohoku District (A; Nos. 2, 4, and 5) were distributed in the second quadrant in the Z_1-Z_2 plain and the third quadrant in the Z_1-Z_3 plain. Two groups (B and C in Fig. 21)

Table 11. Correlation matrix of ten characters.

Characters		X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8	X_9	X_{10}
Plant length	X_1	1.00									
Total dry weight	X_2	0.48**	1.00								
Number of shoots	X_3	-0.12	0.27	1.00							
Number of rhizomes	X_4	-0.13	0.28	0.83**	1.00						
Total rhizome length	X_5	0.30*	0.55**	0.50**	0.75**	1.00					
Rhizome dry weight/X_2 [a]	X_6	0.01	0.22	-0.14	0.29*	0.52**	1.00				
Days to emergence	X_7	-0.71**	-0.29*	0.38**	0.31*	-0.16	-0.11	1.00			
Days to heading	X_8	0.54**	0.09	-0.52**	-0.37*	0.07	0.18	-0.70**	1.00		
Death time of aerial parts	X_9	0.72**	0.31*	-0.19	-0.18	0.22	-0.10	-0.76**	0.66**	1.00	
Days from emergence to death	X_{10}	0.76**	0.32*	-0.27	-0.24	0.21	-0.04	-0.88**	0.71**	0.98**	1.00

* and ** are satistically significant at 5 and 1% level, respectively.
a) arcsin $\sqrt{\text{percentge}}$ transformation was made for statistical calculation.

Table 12. Factor loadings, eigen values, and their contribution percentages to the total variances obtained from principal component analysis of ten characters.

Characters		Z_1	Z_2	Z_3
Plant length	X_1	0.83	0.22	-0.19
Total dry weight	X_2	0.36	0.64	-0.07
Number of shoots	X_3	-0.42	0.73	-0.46
Number of rhizomes	X_4	-0.35	0.88	-0.04
Total rhizome length	X_5	0.18	0.92	0.19
Rhizome dry weight/X_2 [a)]	X_6	0.08	0.40	0.89
Emergence time	X_7	-0.91	0.01	-0.05
Heading time	X_8	0.82	-0.16	0.27
Death time of aerial parts	X_9	0.90	0.09	-0.25
Days from emergence to death	X_{10}	0.96	0.06	-0.17
Eigen value		4.37	2.81	1.25
Accumulative contribution (%)		43.7	71.9	84.4

a) arcsin $\sqrt{\text{percentage}}$ transformation was made for statistical calculation.

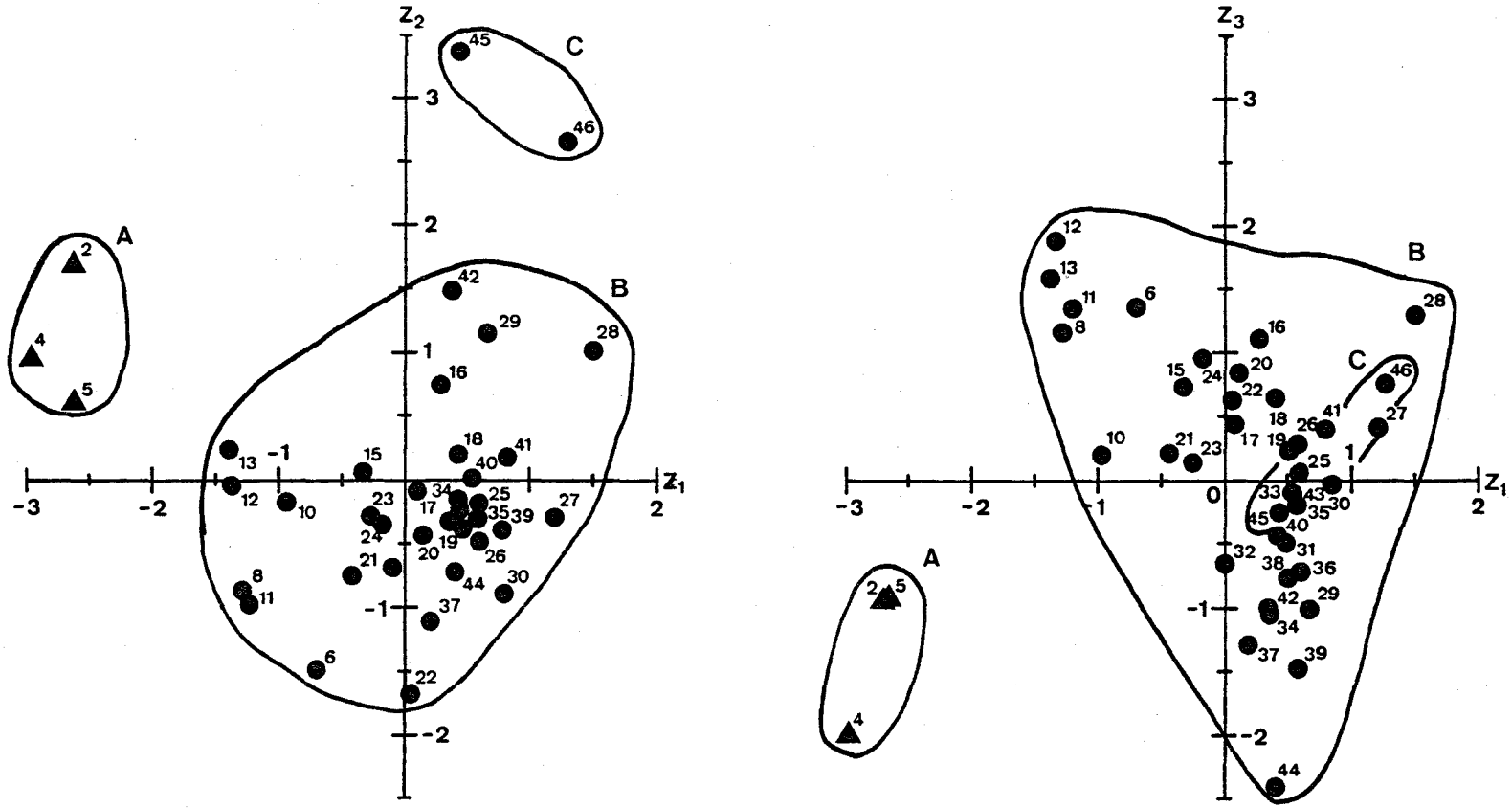

Fig. 21. Scatter diagrams of 47 clones.

Symbols and numbers are the same as in Table 10 and Fig. 13.
Right figure is Z_1-Z_2 plain. Left one is Z_1-Z_3 plain.
A: clones of var. genuina from northern Tohoku District.
B: clones of var. koenigii from southern Tohoku to northern Kyushu District.
C: clones of var. koenigii from southern Kyushu District.

of I. cylindrica var. koenigii from Honshu, Shikoku, and Kyushu District were found in the Z_1-Z_2 plain. Clones from the southern parts of the Tohoku to the northern parts of the Kyushu District (B) were situated around the origin of ordinates. Whereas, clones from the southern parts of the Kyushu District (C; Nos. 45 and 46) were distributed in the first quadrant. In the Z_1-Z_3 plain, groups A and B were clearly distinguished each other, as shown in the Z_1-Z_2 plain, but group C was laid in the range of group B.

Clonal variation in the effects of temperature or photoperiod on heading

In all six experimental plots of temperature and photoperiodic treatments, clones from the northern parts of Japan generally headed earlier than those from the southern parts. The period to heading of all clones used were shortened notably by high temperature and lengthened by low temperature (Fig. 22). But in all photoperiodic regimes, no differences in heading were observed (Fig. 23), except two clones (Nos. 10 and 14). The heading of these two clones, Nos. 10 and 14, was accelerated by short day treatment.

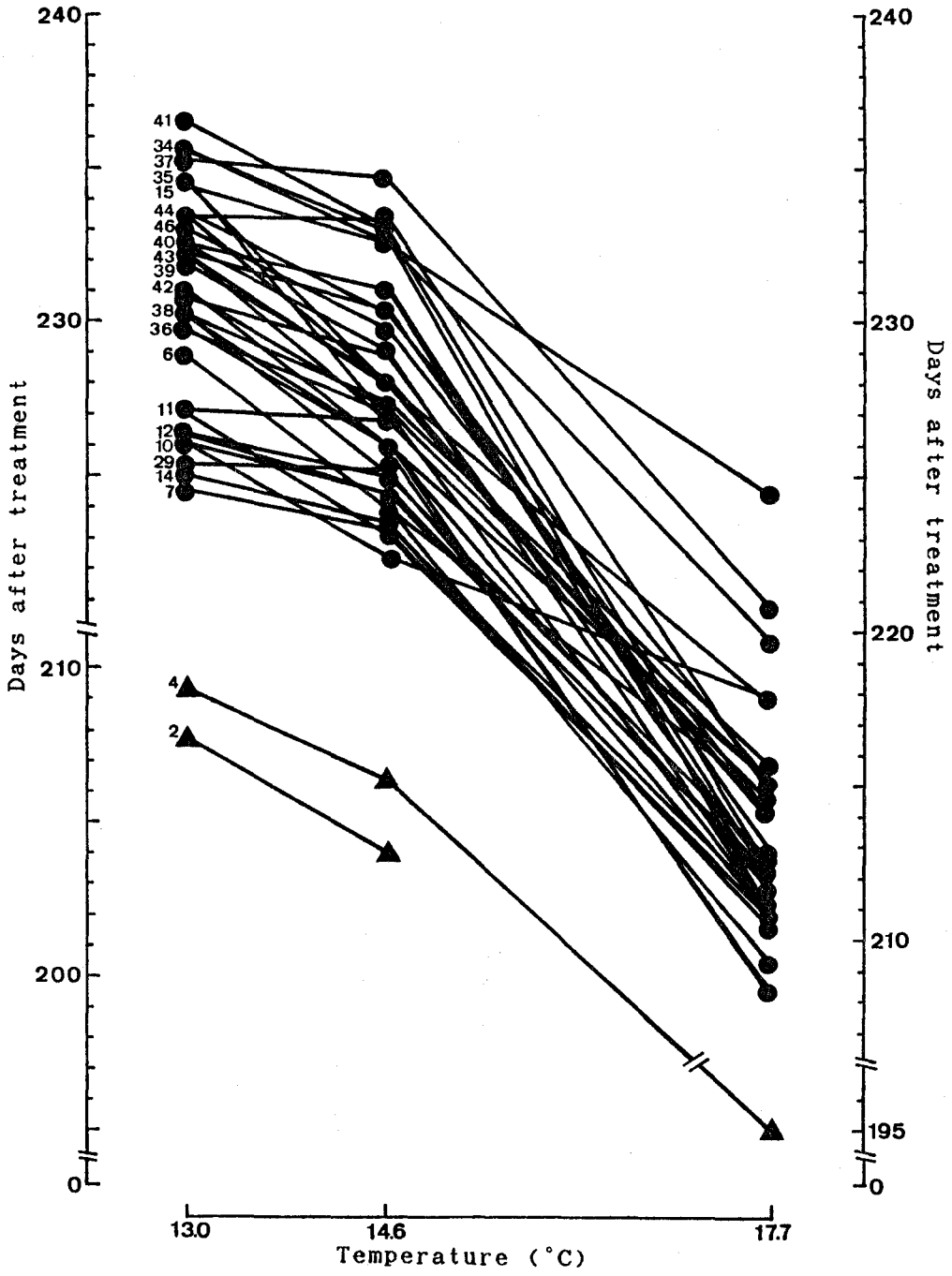

Fig. 22. Effect of temperature on heading date of Imperata cylindrica.

Symbols and numbers are the same as in Table 10 and Fig. 13. Clones No. 1 and 3 which did not head during experiment were not shown.

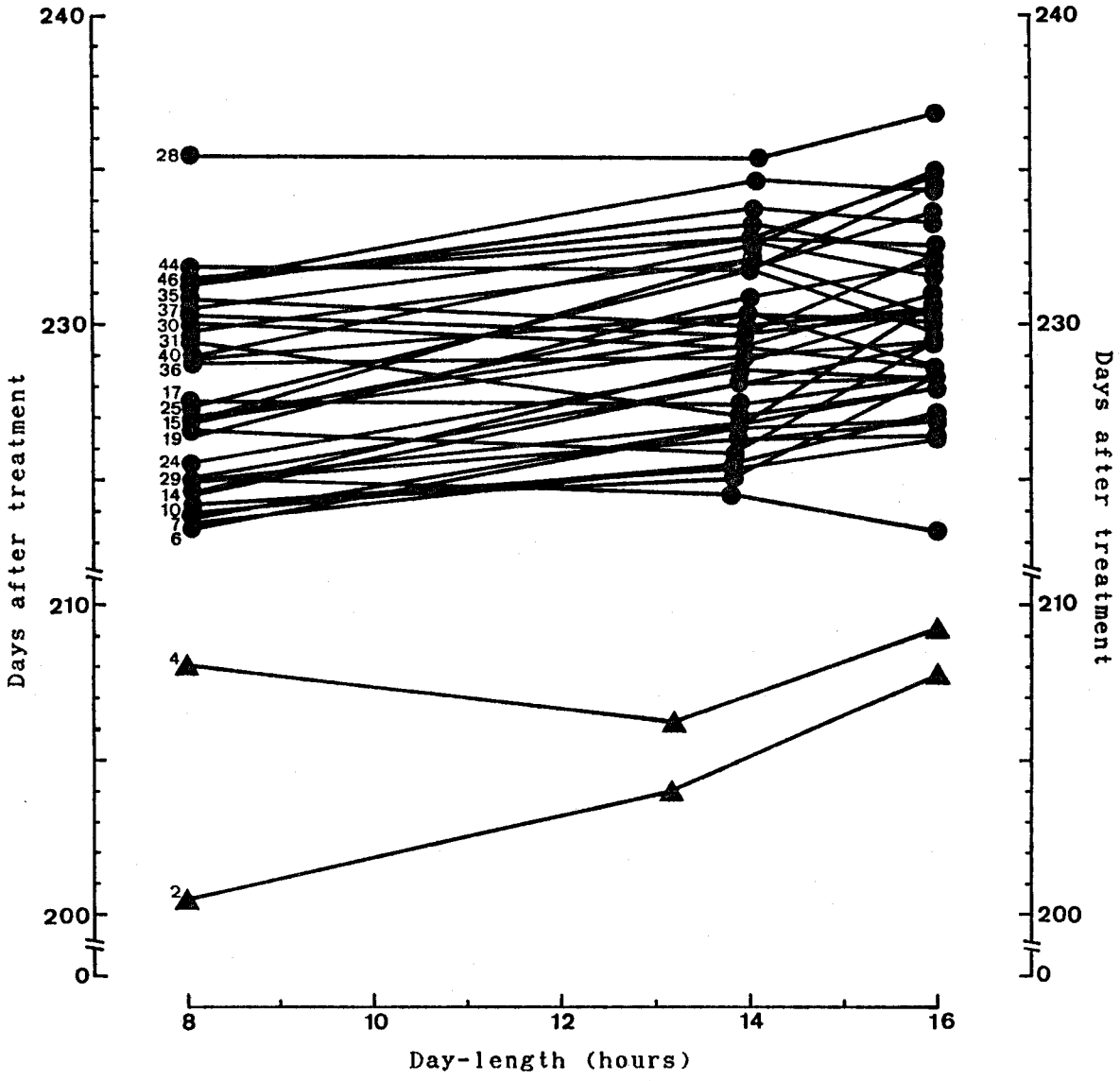

Fig. 23. Effect of photoperiod on heading date of Imperata cylindrica.

Symbols and numbers are the same as in Table 10 and Fig. 13. Clones No. 1 and 3 did not head during experiment.

DISCUSSION

I. cylindrica distributed in Japan is classified into two varieties, var. koenigii (Retz.) Durand et Schinz and var. genuina Durand et Schinz, based on the presence or absence of hairs on node of culm. The present study showed that these two varieties had different geographical distribution. I. cylindrica var. koenigii was distributed in the southern parts of the Tohoku District and southwards. The distribution of var. genuina was confined to Hokkaido, northern parts of Tohoku District, and to highland regions of Central Japan (Fig. 13). The boundary of geographical distribution of these two varieties was generally consistent with that of the summer green broad leaved forest zone and the evergreen broad leaved forest zone as shown in Fig. 13. It almost agreed with the 85 Warmth Index line, and with -20 Coldness Index line proposed by Kira (1949). The similar result was also obtained in Plantago asiatica Linn. (Yamanishi and Fukunaga, 1983). The boundary line of the distribution of the two types, the summer green type and the evergreen type of P. asiatica, was similar to that of the two varieties of I. cylindrica. The distribution of these two varieties is presumable to be determined considerably by temperature.

I. cylindrica var. genuina distributed in the northern and highland regions of Japan have waxy glaucous leaf sheaths. In Eucalyptus urnigera Hook. fil. of Australia, such altitudinal cline in leaf waxy glaucousness was recognized (Barber, 1965). Barber and Thomas (cited in Barber, 1965) described that the glaucous phenotype had a number of important effects on frost-resistance, transpiration in mist, leaf temperature, and so on. Such effects of waxy glaucousness as shown in E. urnigera may be observed in I. cylindrica var. genuina with waxy glaucous leaf sheath in Hokkaido, northern parts of Tohoku District and highland regions of Central Japan. Honda (1930) classified var. genuina into two forms: form. typica Honda with reddish purple leaf sheath and stigma, and form. pallida Honda with slender plant type and with light green leaf sheath and whitish brown stigma. The glabrous clones with waxy glaucous leaf sheath observed in this experiment belong to neither forms, form. typica nor form. pallida; because those clones had slender plant type, waxy bloomy reddish purple leaf sheath and purple stigma. The glabrous clones observed in this experiment were similar to form. pallida in plant type, but their colour of leaf sheath and stigma were resemble to form. typica. They may be the biotype which is adapted to the climatic environment of the northern or highland regions in Japan, judging from their dis-

tribution, phenology, and waxy bloomy leaf sheath.

Matumura et al. (1980) reported the glabrous type of this species in the Nohbi Plain, Central Japan and identified it as I. cylindrica var. genuina form. pallida. The glabrous clones observed in this experiment is not the same as reported by Matumura et al. (1980, 1983, 1984) in the distribution and plant size. The biotype reported in Matumura et al. (1980, 1983, 1984) is not presumably form. pallida but form. typica by its plant type.

The latitudinal cline in the phenology and plant size of I. cylindrica in Japan was shown in this experiment. Clones from the northern parts of Japan were shorter in plant length (Fig. 19), lighter in total dry matter weight (Fig. 20); they emerged later (Fig. 14), headed (Fig. 15) and died (Fig. 16) earlier than those from the southern areas. The similar latitudinal cline in the phenology was obtained in Plantago asiatica (Yamanishi and Fukunaga, 1983) and in the heading date of Echinochloa oryzicola (Yabuno, 1966) and Polygonum thunbergii Sieb. et Zucc. (Sawamura, 1967). Clones of I. cylindrica in the northern parts of Japan generally emerged late in spring and their aerial parts died early in winter. Their dormant stage corresponded to the cold season in their original habitats. On the other hand, clones collected in the Amami and Okinawa District were evergreen. Those clones need not

dormancy even in winter, because they may have enough temperature for growth all over the year. The clinal variation of the plant length and total dry matter weight observed in this experiment seemed partially to be resulted from the cline of the length of growth period. These relationships between latitude or annual mean temperature of original habitat and plant size or phenology of each clone may be attributed to the adaptation to climatic factors in each original habitat. Such climatic factors, the length of cold season and the degree of coldness, may play an important role on the distribution of the two varieties of I. cylindrica.

From the results of principal component analysis (PCA), I. cylindrica var. genuina (A in Fig. 21) and var. koenigii (B and C in Fig. 21) were clearly distinguished and two groups of var. koenigii were recognized: Group B was composed of the clones from the southern parts of the Tohoku to northern parts of the Kyushu District; Group C from the southern parts of the Kyushu District. Such differentiation to some local populations of I. cylindrica as observed in this study was also reported in Iraq (Al-juboory and Hassawy, 1980).

The heading date was greatly affected by temperature (Fig. 22) but scarcely by photoperiod except two clones (Fig. 23). The heading of two clones from Gunma (No. 10)

and Kanagawa Prefecture (No. 14) was promoted by short day treatment. This result is supported by the observation in the natural population. The heading of this species in natural habitat is observed after cutting of the aerial parts besides the flowering season in uncut condition. The long distance dispersal is practiced by seed. Therefore, undecided heading after cutting, not depending on photoperiodic reaction, seems to be reasonable.

The results obtained in this study are summarized as follows: Three types of I. cylindrica were classified, the evergreen type of I. cylindrica var. koenigii found in the Ryukyu Islands, the summer green type of var. koenigii ranging from the southern parts of the Tohoku District to the Kyushu District, and the summer green type with small plant size of var. genuina which distribution was restricted to Hokkaido, northern parts of the Tohoku District, and highland regions of Central Japan. It was also clarified that I. cylindrica in Japan had latitudinal variation in the plant size and phenology and this cline was resulted from the adaptation to the climate in each original habitat. It will be necessary to establish the control programs reflecting the phenology of this weed in each habitat.

Chapter 6. General discussion and conclusion

Imperata cylindrica is widely distributed in the tropics and the warm temperate zone of the world and this is the most noxious upland weed in these regions. Through the series of experiments, vigorous vegetative reproduction by rhizomes (Chapter 2) and the two different modes of variation, one was ecotypic (Chapters 3 and 4) and the other was climatic (Chapter 5), were clarified.

In this chapter, the various modes of adaptation to each habitat of I. cylindrica were discussed based on the results about variation in the morphology, reproductive strategy and phenology studied in the foregoing chapters.

The ecotypic differentiation of this species in the inland and foredune types was summarized in Table 13. The inland type has large plant size and thick rhizomes. This type grew in roadsides and in abandoned fields where man's managements, especially weeding, have been practiced and many other species have been coexisted. In such habitat, the large plant type with thick rhizomes can regrow rapidly because of abundant reserve substances in rhizomes. Therefore, such type may be selected. As shown in Chapter 2, in the natural population of which aerial parts have been cut

Table 13. Comparison of seven characters of clones from inland and foredune populations.

Characters	Clones from inland	Clones from foredune
Habitats	Common in roadside, orchard garden and abandoned field	Confined to foredune
Salt tolerance	Low	High
Pollen fertility	Normal	Sterile
Anther size	Large	Extremely small
Glume length	Short	Long
Plant size	Large	Small
Rhizome diameter	Thick	Slender

frequently, this species grew densely and dominated. The inland type seems to be common in roadside and abandoned field where cutting has been conducted frequently.

Clones in the foredune were small plant type with slender rhizomes compared with the inland ones and were salt tolerant and male sterile. In the foredune, such clones suffer from the strong sea breezes accompanied with the movement of sand uncyclicly and a few other species coexist. The clones of the salt tolerant and small plant type have been selected. Their reproduction was made only by rhizomes, because this type was male sterile. The similar differentiation in maritime habitats was also reported in Hypericum perforatum (Pritchard, 1960) and Agrostis stolonifera (Aston and Bradshaw, 1966).

The another mode of differentiation, the climatic one, was shown in Table 14. I. cylindrica in Japan was divided into three types: The waxy glaucous small type of var. genuina, the summer green one of var. koenigii with dormant stage in winter, and the evergreen one of var. koenigii.

The waxy glaucous small type was distributed in Hokkaido, the northern parts of Tohoku District, and the highland regions of Central Japan. It headed exceptionally early and its growing period was short. The waxy glaucousness was supposed to play an important role in the frost and cold resistance as reported in Eucalyptus urnigera by

Table 14. Characteristics of three types of Imperata cylindrica in this experiment.

	Var. koenigii		Var. genuina
Distribution	Ryukyu Islands	South Tohoku to Kyushu District	Hokkaido, north Tohoku and highlands of Central Japan
Death time of aerial parts	Evergreen	Late	Early
Hairs on node	+	+	-
Waxy glaucousness	-	-	+
Colour of stigma	Purple	Purple	Purple
Colour of leaf sheath	Reddish purple to light green	Reddish purple to light green	Reddish purple
Plant size	Large	Large to medium	Small
Emergence	Most early	Early	Late
Heading time in Kii-Ohshima	May to October	May	April

Barber (1965).

The summer green type of var. koenigii is distributed from the southern parts of the Tohoku District to the Kyushu District. Its plant size and phenology shows the intermediate form between the waxy glaucous type of var. genuina and the evergreen type of var. koenigii described below. The clones of this type were furthermore subdivided into two groups: One collected from the southern parts of Tohoku District southwards to the northern parts of Kyushu District; the other from the southern parts of the Kyushu District. The clones of each group showed resemble plant size and phenology one another.

The evergreen type was distributed in the Amami Islands and southwards. This type was large in plant size and headed intermittently all over the year in the original habitat.

The phenology of each type mentioned above is well consistent with the seasonal changes in the temperature in the original habitat. The main selection pressure differentiating these three types seems to be the climatic factors, especially the temperature in winter.

Two types of adaptive variation, one to the climatic factors and the other to the saline habitat, were found. The wide variation in the morphological characters of I. cylindrica and adaptive ones to the climatic factors may

make the wide distribution of this species possible and give troublesome characteristics.

Summary

Imperata cylindrica is one of the most troublesome grass weeds in the tropics and the warm temperate zone of the world. To clarify the adaptive mode, dry matter production in the natural population and clonal variation in the plant size, morphology and phenology were surveyed. A series of experiments was practiced at the Subtropical Plant Institute of Kyoto University in the Kii-Ohshima Island, located at the southern extremity of the Kii Peninsula.

Dry matter production

The seasonal change in the dry matter production of I. cylindrica var. koenigii grassland was investigated in the abandoned field (135°50'E, 33°28'N, about 50 m above the sea level) in the Kii-Ohshima Island. In this field, this weed grew densely and covered almost all area of the field. The standing crop in three quadrats (50 x 50 cm^2) was investigated by the stratified clipping method at intervals of about one month from June 14th, 1980 to May 18th, 1981.

In the investigated field, I. cylindrica var. koenigii was dominant in all seasons. The maximum standing crop of

883 g/m^2 was obtained in January, and 772 g/m^2 of that was occupied by I. cylindrica var. koenigii. The other 31 species, such as Miscanthus sinensis, Rumex acetosa, and Pteridium aquilinum var. latiusculum etc., covered only a small area. The rhizomes of this grass weed were distributed densely and complicatedly in the 0 to 30 cm deep in the soil. The rhizome dry matter weight occupied 40 to 50% of the total one.

Intra- and inter-populational variation in the Kii-Ohshima Island

To clarify intra- and inter-populational variation of I. cylindrica var. koenigii in the Kii-Ohshima Island, the plant size, morphology, pollen fertility, and seed set percentage were investigated in 11 populations. Five clones as apart as possible from one another in one population were collected and five ramets of each clone, in total, 275 ramets were planted in about 6000 cm^3 pots filled with clay loam on June, 10th, 1983. The seed set percentage in natural population was investigated for three years, from 1982 to 1984.

The seed set percentage in the natural population notably varied among populations and among three years. The one of foredune population was very low, 0.10 to 0.46%, because of the male sterility. In the other ten popula-

tions, a wide range of seed set percentage was observed from 1.05 to 59.07% and it was attributable to the population size and/or the density of heading panicles, for pollen fertility of each population reached 94.08 to 99.15%.

Under cultivated condition, the selfing ratio of each clone was 0.00 to 0.35% and 100 kernel weight showed 11.07 to 13.15 mg. No differences within population were observed in the plant length, total dry matter weight, number of shoots, total rhizome length, weight per length of rhizome, anther size and dry matter partitioning ratio to rhizome, though significant differences were obtained among populations. One randomly sampled clone was representative of the population. This suggest that one clone per population was enough in number for assessing morphological differences among populations. The variability within population was smaller in foredune population than in the other ten populations.

Differences between inland and foredune populations in the Kii Peninsula

To compare the morphological characters and pollen fertility of the clones from inland populations with those from foredune ones of I. cylindrica var. koenigii, 33 clones from 17 inland and 16 foredune populations in the

Kii Peninsula were studied and five ramets from one clone per one population were planted in the about 6000 cm^3 clay pots filled with clay loam on June, 1984. Plant length, dry matter weight of each organ, length and diameter of rhizome, number of shoots and rhizomes were measured in mid-November. The seed set percentage of each population was investigated in the original habitat in mid-June, 1984.

Under cultivated condition, the significant differences between inland and foredune populations were detected in the plant size and morphology. The clones from inland populations were significantly longer in plant length, larger in the diameter of rhizome, heavier in leaf, rhizome and total dry matter weight than those of foredune populations. Foredune populations had smaller anther and longer glume than those of inland populations. The seed set percentage of inland populations in original habitat indicated 4.3 to 73.3%. On the other hand, those of foredune populations were less than 3.6%, because of the male sterility.

These genetic differences may be the results of the selection such as cutting, competition with the other species, or salt spray from the sea.

Geographical variation in Japan

To make clear the geographical variation in the mor-

phology and phenology of I. cylindrica in Japan, 388 clones, one clone from one population, were collected from Hokkaido and southwards to Okinawa Prefecture. Dry matter production, heading response to temperature and day-length of 52 clones out of 388 clones were also examined in 1985. Five and three ramets of each clone were used in the dry matter and heading response experiment, respectively. Principal component analysis of the ten characters of plant size and phenology was practiced for 45 clones from Honshu, Shikoku, and Kyushu District.

Latitudinal cline was found in the plant size and phenology of this weed. The clones from northern parts of Japan were smaller in plant size, emerged later, and their heading time and death time of aerial parts were earlier than those from southern parts. Though the heading time of almost all clones was not affected by long day (16 hours day-length) and short day (8 hours) treatment, it was promoted by high temperature (mean temperature, 17.7 ℃); however it was delayed by low temperature (13.0 ℃) compared with that of medium temperature plot (14.6 ℃). The clinal tendency in such responses was not observed.

The clones used in this experiment were clearly divided into two varieties based on the presence or absence of hairs on node of culm. Glabrous clones, var. genuina, were confined to Hokkaido, northern parts of Tohoku Dis-

trict and highlands of Central Japan, and they headed exceptionally early. On the other hand, hairy clones, var. koenigii, were distributed in the southern parts of Tohoku District and southwards. This variety was divided into two types based on the phenology. Clones from the Amami Ohshima Islands and southwards were evergreen and headed intermittently in May to October in the Kii-Ohshima Island. Whereas, clones from the southern parts of Tohoku to Kyushu District became dormant in winter and headed once a year, in May. Furthermore, according to the results of principal component analysis of the ten characters, these clones were subdivided into two groups. Such differentiation is attributed to the differences in the climatic factors, especially temperature.

This grass weed showed vigorous vegetative reproduction by rhizomes. This species had wide intraspecific variation and the groups subdivided in this experiment were to adapt to each habitat. Those characteristics of this weed may cause the difficulty in the control and wide distribution in Japan.

Acknowledgements

The author wishes to thank Dr. K. Ueki, Professor of the Laboratory of Weed Science, Kyoto University, for his guidance and encouragement during the course of this work. He is also greatly indebted to Dr. H. Kobayashi, the Laboratory of Weed Science, Kyoto University, for his continuous guidance, advice, and various help.

The author would like to express his sincere thanks to Dr. S. Shigenaga and Dr. M. Fujimoto, the Subtropical Plant Institute, Kyoto University, for their hearty encouragements. He is also grateful to Dr. M. Ito and Mr. Y. Yamasue, the Laboratory of Weed Science, Kyoto University, for their helpful advice. Thanks are due to all members of the Subtropical Plant Institute, Kyoto University, for their helps given in various ways.

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